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Seattle, Washington

U.S. DEPARTMENT OF COMMERCE

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NATIONAL MARINE FISHERIES SERVICE

Fishery Bulletin

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DIEL FEEDING PATTERNS OF 16 SPECIES OF MESOPELAGIC FISHES FROM HAWAIIAN WATERS

THOMAS A. CLARKE[1]

ABSTRACT

Diel patterns of stomach fullness, as percent of dry weight, were determined for 16 species of mesopelagic fishes. Nine species of myctophids and one melamphaid, all vertical migrators, appeared to feed solely or principally at night in the upper layers. These species encountered higher temperatures and prey concentrations at night. Four species of stomiatoid fishes appeared to feed during the day regardless of the extent of their migration or the absence thereof. Prey concentrations encountered by the stomiatoids during the daytime appeared to be higher than or similar to those encountered at night. One myctophid and one gonostomatid showed no diel pattern; diel changes in the environmental factors considered were relatively small in spite of the fact that both species undertook limited vertical migrations.

Crude estimates of instantaneous evacuation rate and daily ration were made from data for four species. These indicated that evacuation rate was increased at night in the upper layers and that daily rations of species which migrated into the upper layers were similar to values for shallow-living zooplanktonivores, while rations of deeper living species were lower. Thus while the adaptive value of upward migration in the species which feed at night is obviously related to feeding activity, the upward ascent by the daytime feeders may allow processing of larger daily rations than if they remained at low temperature all day.

The extensive diel vertical migrations of certain mesopelagic fishes have been well documented in a variety of oceanographic situations. While a number of theories have been proposed to explain the adaptive value of the behavior—in both fishes and migrating invertebrates as well—data to support any of them are few. One of the most frequently proposed hypotheses (e.g., Marshall 1960) is that the organisms ascend at night to feed in the upper layers where food is presumably at higher concentrations and descend during the day to avoid predation while the upper layers are well lighted. Several studies of mesopelagic fishes (to be cited below) have considered the relationship between feeding chronology and vertical distribution in an effort to support at least one-half of the hypothesis, but the results have for the most part been rather equivocal. Apparent diel trends in stomach fullness or details thereof are often questionable owing to low numbers of specimens examined, insensitive methodology, or incomplete diel coverage. Furthermore, all such studies on mesopelagic fishes, with the exception of Merrett and Roe (1974), have been conducted in high latitude or neritic situations and have dealt with only one or, at most, three species.

This study considered the feeding chronology of 16 species from 5 families of mesopelagic fishes from the north central Pacific Ocean. Vertical distribution and certain other apsects of the ecology of these fishes are covered in Clarke (1973, 1974) and Clarke and Wagner (1976); results from related investigations in the same study area are summarized in Maynard et al. (1975). Comparison of diel patterns of stomach fullness and diel changes in temperature and prey concentration allow consideration of adaptive value of the vertical migrations undertaken by most of these species. In four species, rough calculations of daily ration are possible using equations similar to those presented by Eggers (1977).

MATERIALS AND METHODS

Field Sampling

Specimens for this study were all collected with a 3-m Isaacs-Kidd midwater trawl ca. 20 km west of the island of Oahu, Hawaii (ca. lat. 21°20-30′N; long. 158°20-30′W) in waters 2,000-3,000 m deep. In order to reduce the concentration of zooplankton in the cod end of the net and thus

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minimize bias due to fishes' feeding after capture, the net terminated in a 1-m diameter cone of ca. 3-mm (⅛-in) knitted nylon mesh instead of the "normal" plankton netting.

Specimens were taken in oblique tows which sampled vertically migrating species at nine different periods of the 24-h cycle. At night, cable was paid out in increments over a period of 1.5 h such that the trawl fished roughly equal amounts of time at all depths between the surface and ca. 350 m. The trawl was retrieved immediately afterwards for a total towing time of about 2 h. Four such tows were made between last light at dusk and first light at dawn. During the day, 1,200 m of wire were paid out initially. This placed the trawl at ca. 350-400 m. Subsequently, cable was paid out in increments such that the trawl fished between this depth and ca. 1,100-1,200 m over a period of 1.5 h and then retrieved for a total fishing time of ca. 2.5 h below 350-400 m. Three such tows were made during the day. At dusk, 1,500 m of cable were paid out initially, placing the trawl at ca. 500 m. Cable was then retrieved in increments such that the trawl fished between 500 m and the surface over 1.5 h. The trawl reached maximum depth just before sunset and was on deck shortly after last light. At dawn, the process was reversed, and the trawl shot before first light, and fished from the surface to ca. 500 m over 1.5 h such that it reached maximum depth ca. 1 h after sunrise. Ship speed was ca. 1 m/s (2 kn) for cable retrieval and ca. 2 m/s (4 kn) for all other phases.

In order to collect sufficient numbers of specimens for as many species as possible, three 24-h series of nine tows each (dusk, four at night, dawn, and three during the day) were made 27-30 August 1973. These dates were chosen to bracket new moon (August 28) and minimize avoidance of the trawl at night (Clarke 1973). One day tow of this series was fouled and could not be repeated until 13 September 1973. The total range of time fished by equivalent tows of each series (Table 1) overlapped—considerably so for the night series due to one night's fishing proceeding ahead of schedule. The overlap was effectively less than shown in Table 1 since most of the fishes analyzed were probably taken below 50 m (based on previously cited studies of vertical distribution) and not during the first 15 min or the last 5 min of each tow when the trawl was shallower than 50 m. Consequently, equivalent tows from each 24-h series were considered replicates and specimens were combined for data from each period. The nine sampling periods will subsequently be designated as follows: SS for sunset and SR for sunrise; N1, N2, N3, N4 for the four night periods in chronological sequence; and D1, D2, D3 for the three daytime periods in sequence.

Danaphos oculatus, a nonmigrating species, was not taken in the shallow night tows described above. Nighttime data for this species were based on specimens from three night series of three tows each taken 30 August-1 September and 13-14 September 1973 (Table 1) using the same towing schedule described above for daytime (ca. 400-1,000 m). Thus only eight periods of the diel cycle were considered. The three nighttime periods for *D. oculatus* were designated dN1, dN2, and dN3.

In order to obtain more specimens of three species of stomiatoids, I utilized specimens taken 24-25 May 1974 in seven tows at the same location with the same net, and with the same procedure and timings as N1-4 and D1-3. The numbers of specimens used from this series will be noted in the results. All specimens of the other species came from 1973 collections.

The catch was immediately preserved in 4-5% formaldehyde in seawater. The specimens remained in this solution for up to 2 yr before processing, but since all specimens of a given species were processed within a period of 2-3 wk, any between-sample differences in weight loss due to leaching can be considered negligible.

Laboratory Analyses

The ratio of the dry weight of the stomach contents to that of the fish as percent was used as an index of stomach fullness. Where sufficient specimens of a given species were available, 20 from each of the nine sampling periods were examined. If possible, the least damaged specimens (or perhaps more appropriately—equivalently damaged specimens) were selected from a narrow size range. For many species, however, it was necessary to use specimens damaged to various degrees and of all sizes between recently (but fully) metamorphosed juveniles and mature adults. In cases where a specimen was damaged beyond loss of scales or fin rays, i.e., where tissue was missing, I used the median dry weight of other specimens of the same standard length.

Each fish was briefly rinsed with tapwater and gently blotted; standard length was measured to the nearest millimeter. The stomach (anterior end of the esophagus to the pyloric valve) was removed

TABLE 1.—Towing times (Hawaiian Standard Time) for three 24-h series of oblique tows to sample vertically migrating mesopelagic fishes and three all night series for deep-living nonmigratory fishes. Times given for dusk (SS), dawn (SR), and shallow night (N1-4) are for the entire tow; those for day tows (D1-3) and deep night tows (dN1-3) are for the time the trawl fished below ca. 350-400 m.

Period	27-28 Aug.	28-29 Aug.	29-30 Aug.	Midpoint	Period	30-31 Aug.	31 Aug.-1 Sept.	13-14 Sept.	Midpoint
SS	1754-1956	1815-1955	1820-2023	1910	dN1	2040-2300	2005-2233	2000-2235	2130
N1	2045-2240	2001-2155	2040-2233	2120	dN2	2352-0215	2325-0154	2330-0155	0050
N2	2315-0110	2207-0005	2255-0045	2340	dN3	0308-0540	0250-0515	0255-0525	0415
N3	0120-0320	0015-0210	0113-0310	0150					
N4	0330-0520	0220-0420	0318-0515	0350					
SR	0535-0742	0515-0725	0533-0745	0630					
D1	0822-1047	0807-1034	0820-1045	0930					
D2	1143-1425	1125-1350	1135-1410	1300					
D3	1510-1740[1]	1448-1710	1515-1740	1615					

[1]The D3 tow for 28 August was fouled; time given is for tow made on 13 September.

and its contents, if any, placed on a clean glass slide. The fish including the empty stomach was placed in a preweighed aluminum pan. After examination, the stomach contents were rinsed into a second preweighed pan using distilled water.

The stomach contents were examined only casually. A rough estimate of fullness was made and degree of digestion noted. Prosome length (PL) of copepods and total length (TL) of other prey were recorded from intact items. Intact prey items could usually be identified to genus, but no serious attempt was made to determine composition of the diet from these samples. The remarks below on types of prey include only the most frequently encountered items and are not meant to be taken as detailed analyses of diets.

Both fish and stomach contents were dried at 60°C for 24 h (somewhat longer for a few large fish) and allowed to cool under partial vacuum before weighing. The pans with stomach contents were weighed to the nearest 0.01 mg on a microbalance, and the content weight determined by subtraction. Both control pans and reweighing of several pans with dried stomach contents after a second period in the drying oven or desiccator indicated that the weighing and handling error was of the order of ±0.02 mg. There was no indication that error was proportional to the amount of material in the pan. Pans with fish were weighed on a semimicro balance; the reading was recorded to 0.01 mg on small fish and to 0.1 mg on those over ca. 100 mg. Based on changes in weight of control pans and reweighing of fish after a second period of desiccation, the error was <1% of the fish weight.

While the weighing and handling error was such that estimates of stomach fullness were affected only to the fourth or possibly third decimal place, other errors or biases inherent in the material should be mentioned. As noted above, an unknown fraction of the material was lost due to leaching. Damage to the fish positively biased the ratios since there was some loss of skin, scales, or fin rays in almost all specimens. Such errors were unrelated to the time of collection and were more likely to increase variability and thus to obscure rather than cause diel trends in the data. The intestinal contents, which were dried and weighed with the fish, may have varied with time and thus introduced a systematic error in fish weights. Based on visual examination, however, largest amounts of materials in the intestine were almost certainly <1% of the total fish weight, and, consequently, affected the stomach fullness index by <0.1%.

The 2-3 h durations of the tows were a possible source of bias and high variability. Bias in stomach fullness could result from evacuation of stomach contents between capture and death (Eggers 1977). It is likely that this was negligible since the fishes considered here were probably dead soon after capture by the net. The 2-3 h possible differences in capture time for fishes from the "same" period of the diel cycle almost certainly contributed to the variability in stomach fullness—particularly during periods when the latter was changing rapidly.

Stomach fullness could possibly be biased negatively by regurgitation after capture or positively by feeding in the net. (Either type of bias would tend to obscure rather than cause diel differences in stomach fullness.) Regurgitation apparently occurred infrequently in all species considered except *Lampanyctus nobilis*. Except for the latter (see below), specimens with partially digested food remains in the mouth or everted stomachs were not used. Hopkins and Baird (1975) showed that feeding in the net is an unimportant source of error even when a fine-mesh cod end is used, and there was little indication of net feeding in the present study. Zooplankton in good condition, usually crustaceans with appendages erect and extended, were infrequently found in the mouth. These were assumed to have lodged there during

capture and were not counted, but the fish and any other contents were used. Items part way down the esophagus with appendages flattened against the body or the body folded were assumed to have been eaten before capture and were included. I considered such "esophagus" items unlikely to have been eaten after capture because concurrent analyses of diet (Clarke in prep.) on the same species collected by the same net indicate that there is no difference in species composition between such items and items clearly in the stomach and partially digested.

Stomach fullness values for a single species and single time period were rarely distributed normally. Usually the values were skewed to the left, but variably so — the mean being sometimes close to the median and sometimes close to the 75th percentile. Consequently, the entire set of stomach fullness values for each species were ranked and tested for between-period differences by the Kruskal-Wallis nonparametric equivalent of analysis of variance (H-test). The test is mainly sensitive to differences in position (Tate and Clelland 1957), and significance implies differences among the medians for the separate time periods but does not single out which sets of data are different. Each adjacent (in time) pair of data sets was tested for differences in the median with the Mann-Whitney or Rank sum test (Tate and Clelland 1957); however, because of multiple testing on the same data, the significance levels from this cannot be taken rigorously.

Neither test used is sensitive to differences in variability, and no separate testing was done. Some idea of differences in frequency distribution can be gleaned from relative position of the mean and median. Other gross differences, e.g., bimodality vs. unimodality, will be pointed out in the results. Likewise, I did not test for possible correlations between sex or size of the fish and stomach fullness. The data from each period were, however, ranked and compared (by inspection) with sex and rank in length; no obvious correlations were found.

RESULTS

A total of 15 vertically migrating species (10 myctophids, 4 stomiatoids, and 1 melamphaid) and 1 nonmigrating stomiatoid were investigated. These included species for which 20 individuals were collected at most of the nine periods sampled plus a few, less frequently taken species selected to give broader coverage with respect to systematic position or vertical distribution pattern. In addition to graphical presentations (cited specifically below), ancillary data for all species are summarized in Table 2. In the subsequent presentation, stomachs were considered "empty" if stomach fullness was <0.1%. This included both visually empty stomachs and those with only a trace of digested remains in the pyloric end of the stomach. Types of prey organisms, state of digestion, and other aspects not obvious from the figures or Table 2 are considered in individual species accounts below.

Comments on vertical distribution of prey items are based on preliminary analyses of opening-closing plankton tows taken in the study area and their general agreement with data in the literature for the same or closely related species in other central water mass localities. The plankton tows—16 taken in September 1973 and 20 in November 1974—covered the depth ranges of the fishes considered both day and night. Euphausiids from all samples have been counted and identified, and copepods either counted (shallow night samples) or sufficiently examined to at least roughly determine the depth ranges of the important prey species. The apparent depth ranges agree generally with those given by Brinton (1967) and Roe (1972). These two important types of prey can, with a high degree of certainty, be classified as shallow nonmigrators (above 200-300 m both day and night), vertical migrators (above 200-300 m at night and below this depth by day), and deep living (below 300 m day and night). Similar statements cannot be made for ostracods, the other important crustacean group, nor for other taxa of zooplankton.

Myctophidae

Benthosema suborbitale (Figure 1)

The H-test indicated highly significant ($P<0.005$) differences in stomach fullness over the diel cycle. The data from SS and N1 were characterized by low averages, narrow percentile limits, and high proportions of empty stomachs. Subsequently stomach fullness generally increased until SR and decreased throughout the day. The most frequent prey items were copepods of the genera *Pleuromamma, Candacia,* and *Paracandacia. Euphausia* spp. and occasionally small decapods contributed significantly to the weight of

TABLE 2.—Summary of data for each of the 16 species of fishes examined from each of the periods of the diel cycle. In each species/time block, the first line gives the number of specimens examined and the number with stomach fullness <0.1% of fish dry weight in parentheses; the second line, the size range of the specimens in millimeters standard length; and the third, the range of stomach fullness values in percentage of fish dry weight. All values of stomach fullness are rounded to the nearest 0.1%.

Species	SS	N1	N2	N3	N4	SR	D1	D2	D3
Benthosema suborbitale	20(12)	20(8)	20(3)	20(1)	20(5)	19(2)	20(2)	20(3)	20(2)
	24-30	15-32	18-31	19-29	22-31	17-27	16-30	18-32	17-30
	0-0.9	0-2.8	0-6.0	0.1-2.7	0.1-2.8	0-2.6	0.1-3.6	0-3.8	0-2.2
Bolinichthys longipes	20(7)	20(2)	20(2)	20(0)	20(1)	20(0)	20(0)	20(0)	20(0)
	24-46	21-46	20-51	17-49	18-43	21-32	16-50	17-46	19-48
	0-1.4	0.1-2.0	0.1-2.5	0.2-1.5	0.1-2.4	0.3-4.6	0.2-4.8	0.1-1.5	0.1-1.1
Ceratoscopelus warmingi	20(9)	20(1)	20(2)	20(2)	20(0)	5(0)	20(1)	20(0)	20(2)
	22-53	18-45	24-45	23-50	25-47	18-23	19-48	19-59	18-52
	0-2.8	0.1-9.8	0-8.1	0-5.0	0.1-7.6	0.9-4.9	0.1-2.4	0.1-4.5	0.1-7.4
Diaphus schmidti	20(2)	20(2)	20(0)	20(0)	20(0)	20(0)	20(0)	20(0)	20(2)
	25-39	20-41	19-41	19-40	17-38	20-38	14-37	15-38	19-38
	0.1-2.3	0.1-1.7	0.3-1.4	0.2-6.0	0.3-3.8	0.1-2.2	0.2-2.3	0.2-2.7	0-2.3
Hygophum proximum	20(14)	20(0)	20(2)	20(1)	20(0)	20(14)	20(16)	20(13)	18(11)
	26-33	19-32	18-38	18-42	18-37	19-43	19-42	19-40	18-46
	0-1.0	0.2-6.7	0-5.8	0.1-3.6	0.2-7.0	0-0.5	0-0.4	0-1.3	0-1.3
Lampanyctus niger	20(14)	20(11)	20(7)	20(8)	20(4)	0	20(10)	20(11)	20(10)
	65-84	65-85	63-83	64-85	51-85	—	52-87	68-85	64-85
	0-1.9	0-1.0	0-1.7	0-1.3	0-1.5	—	0-4.0	0-3.7	0-3.9
Lampanyctus nobilis	9(4)	20(3)	20(2)	20(4)	20(1)	0	14(2)	14(4)	18(6)
	24-84	29-81	27-88	24-80	26-98	—	25-94	25-90	25-94
	0-6.2	0-3.3	0-7.5	0-8.5	0-5.5	—	0-3.6	0-10.3	0-2.0
Lampanyctus steinbecki	20(2)	20(4)	20(3)	20(1)	20(0)	20(2)	20(0)	20(4)	20(2)
	25-39	22-48	22-41	21-39	22-42	18-36	22-42	23-44	27-42
	0-2.7	0-3.7	0-4.4	0-3.5	0.2-4.0	0.1-9.8	0.1-4.5	0-2.1	0-5.5
Notolychnus valdiviae	20(0)	20(1)	20(3)	20(0)	20(0)	20(0)	20(2)	20(1)	20(0)
	19-24	20-23	19-23	19-23	18-23	19-24	20-23	17-22	19-24
	0.2-3.4	0.1-2.9	0-3.0	0.3-4.7	0.3-3.6	0.3-3.5	0-1.7	0-2.5	0.1-3.5
Triphoturus nigrescens	20(3)	20(6)	16(3)	15(3)	19(0)	20(0)	20(4)	20(3)	20(4)
	18-34	17-31	15-34	15-35	16-33	15-36	16-34	18-33	18-34
	0-5.9	0-3.6	0-9.0	0-6.6	1.0-14.3	0.7-9.9	0-16.0	0-6.7	0-4.5
Melamphaes danae	3(0)	12(3)	14(2)	12(0)	9(0)	0	3(0)	2(0)	14(1)
	16-20	16-21	16-21	16-21	16-22	—	19-21	16	16-22
	0.4-0.6	0-3.2	0-3.0	0.4-3.5	0.5-4.0	—	0.3-1.5	1.1-1.5	0-1.6
Gonostoma atlanticum	4(0)	20(2)	20(1)	20(2)	17(4)	7(2)	9(0)	20(1)	8(0)
	48-58	36-62	32-65	31-64	26-62	48-65	22-64	50-68	48-57
	1.1-3.3	0-6.3	0-4.5	0.1-4.3	0-3.5	0.1-1.6	0.3-2.4	0.1-4.6	0.4-11.2
Gonostoma elongatum	20(2)	20(2)	20(1)	20(9)	20(3)	8(0)	20(4)	14(3)	10(1)
	26-112	31-126	30-135	30-132	32-79	30-150	24-125	30-149	29-87
	0.1-2.6	0-13.1	0.1-5.9	0-5.0	0-2.0	0.2-8.0	0-16.6	0-5.2	0.1-7.3
Vinciguerria nimbaria	20(0)	20(0)	20(3)	20(3)	20(13)	20(15)	20(9)	20(1)	20(2)
	21-34	24-35	24-36	25-32	23-34	24-33	20-35	20-33	20-30
	0.7-8.9	0.2-8.9	0-7.9	0-3.1	0-0.6	0-1.8	0-12.7	0.1-6.3	0.1-14.2
Danaphos oculatus	15(0)	9(0)	11(0)	11(0)		15(2)	20(2)	4(0)	10(0)
	27-40	27-39	29-40	29-36		28-42	31-40	28-38	27-39
	0.5-2.5	0.6-2.3	0.3-1.0	0.3-1.8		0-0.8	0-1.0	0.6-1.7	0.2-2.3
Valenciennellus tripunctulatus	6(0)	20(0)	12(0)	9(2)	10(1)	3(2)	7(2)	5(0)	10(0)
	25-30	22-32	23-32	21-32	21-32	21-31	25-30	21-30	22-33
	1.2-4.5	1.2-3.6	0.9-2.2	0-2.2	0.1-1.0	0-0.2	0-0.6	0.9-2.5	1.0-3.5

food. The food from specimens taken by day samples was generally well digested; except for the thoracic spots or "buttons" from *Pleuromamma*, prey was rarely recognizable beyond general category.

Bolinichthys longipes (Figure 1)

Analyses of *B. longipes* were complicated by the frequent presence in the stomachs of digenetic trematodes. These were 1-10 mm long (most were 1-5 mm) and occurred in 41% of the stomachs examined. They were mingled with the food and appeared to have been fixed while wrapping around or holding to items. As a probable consequence, whole prey were rarely found in *B. longipes*' stomachs. The parasites were, however, easily separated from the food; they were not included with either the fish or stomach content weight.

The number of trematodes was roughly a function of size of the fish. Fish < ca. 30 mm SL usually had 0-2 individuals while several > 40 mm contained 10-20. Since there was little between-period difference in size composition of the fish examined, there was no apparent correlation of trematode number with time of day. Also there

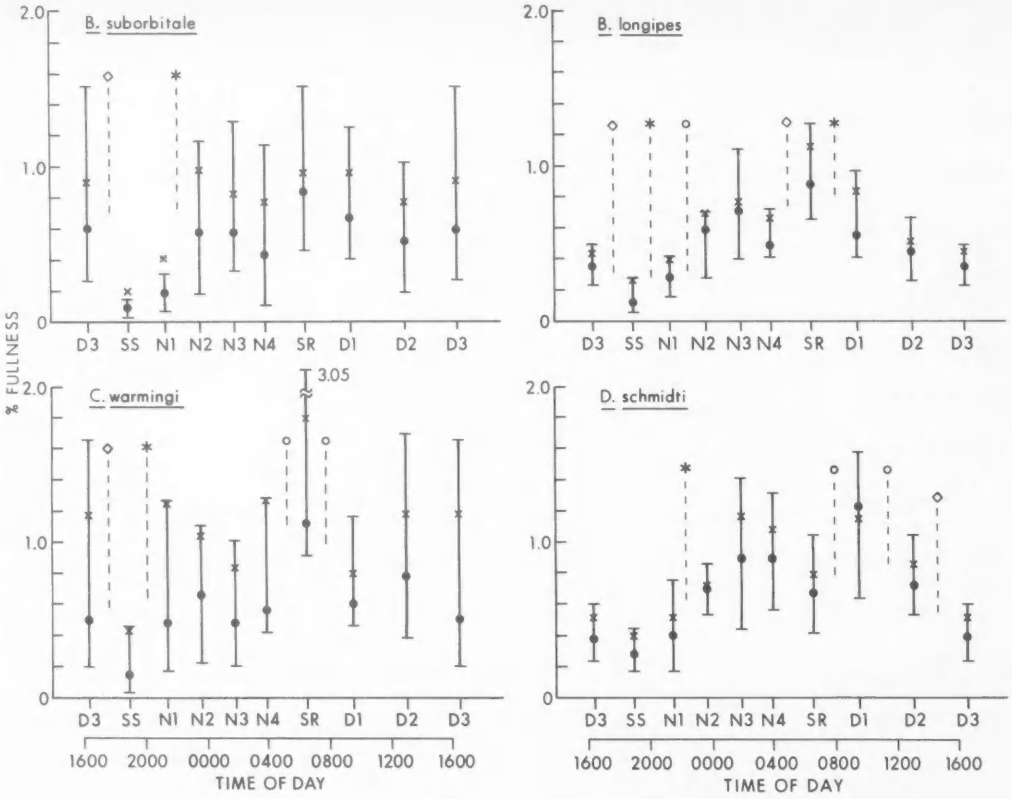

FIGURE 1.—Medians (dots), means (×'s), and ranges between 25th and 75th percentiles (solid vertical lines) of stomach fullness as percentage of body weight throughout the diel cycle for four species of myctophids: *Benthosema suborbitale, Bolinichthys longipes, Ceratoscopelus warmingi,* and *Diaphus schmidti.* Values are positioned at the midpoint of each sampling period (Hawaiian Standard Time). Dashed vertical lines indicate significant differences between adjacent pairs (circle—$0.05<P<0.10$, *—$0.01<P<0.05$, diamond—$P<0.01$; two-tailed probabilities, Rank Sum test).

was no apparent correlation between number of trematodes and amount of food in the gut.

There were highly significant differences ($P<0.005$) in stomach fullness over the diel cycle. The medians and means both showed a trend similar to that of *B. suborbitale* but more of the adjacent pairs showed significant differences and the changes in variability were not as great as with the latter species. The percentage of empty stomachs was <10% at all periods except SS (35%).

Small euphausiids, *Pleuromamma,* and a variety of small (< ca. 2 mm PL) copepods occurred in the stomachs. Even though the stomach parasites apparently broke up the prey items soon after ingestion, there were identifiable pieces of prey in the stomachs from night or dawn. In contrast, contents from day-caught specimens (particularly D2 and D3) were usually amorphous pink material; even the apparently resistant *Pleuromamma* buttons occurred infrequently.

Ceratoscopelus warmingi (Figure 1)

There were significant ($P<0.01$) diel differences in stomach fullness for *C. warmingi.* Similar to the above two species, median stomach fullness was lowest at SS and peaked at SR with an apparent decline in between. The peak at SR, based on only five specimens, differed marginally ($P<0.10$) from values before or afterwards. Day values were comparable with those at night and showed no clear

trend. Except for SS, the percentage of individuals with empty stomachs was low, and there were some fish with very full stomachs (>2%). Because of the latter, ranges and percentile limits were broad, and means were much higher than medians.

Ceratoscopelus warmingi fed on a wider variety of taxa and sizes of prey than did the other species covered here. The most frequent items were copepods, ostracods, and small euphausiids, but heteropods, siphonophores, and other zooplankton also occurred. Intact items of such relatively small prey were recorded mostly from specimens collected at night; remains from day-collected specimens were usually well digested. *Ceratoscopelus warmingi* also took items up to 10% of bodily weight; squid, other fishes, and large euphausiids or decapods occurred in specimens >35-40 mm. Such single large items accounted for nearly all the fish with high values of stomach fullness, and intact prey of this size occurred at all times of the day. Most such items were vertically migrating species that could have been taken at night, but remains of nonmigrating *Cyclothone* spp., which could have only been encountered between dawn and dusk, were found in 11 specimens. Thus, while the overall trend of the data indicates that *C. warmingi* feeds principally on small zooplankton in the upper layers at night, it probably takes large prey whenever encountered.

Diaphus schmidti (Figure 1)

Diel differences in stomach fullness for *D. schmidti* were highly significant ($P<0.005$), and the trend was similar to that of the preceding myctophids except for timing; the maximum value occurred at D1 instead of SR. Empty stomachs occurred only in a few specimens from D3, SS, and N1. *Diaphus schmidti* took a large variety of prey items; the dominant taxa were small crustaceans (ca. 0.5-3.0 mm PL or TL): ostracods, copepods, and larval and juvenile malacostracans. Heteropods, pteropods, polychaetes, and chaetognaths were also noted. Excepting chaetognaths, few items were >4-5 mm. Frequency of intact items was highest at SR, and lowest at D3 and SS.

Hygophum proximum (Figure 2)

Diel differences in stomach fullness for *H. proximum* were highly significant ($P<0.005$), and the trend quite different from those of the other species examined here. Most stomachs were empty, and even 75th percentile values were zero or nearly so between SR and SS; the peak value occurred at N2. *Hygophum proximum* fed principally on medium-sized copepods (1-3 mm PL) and occasionally other crustaceans. Less than 10% of the stomachs were empty for any of the night periods, but intact items were found frequently only in stomachs from N1. By N2 most of the prey were unrecognizable, and only six items were recognizable to even general category in all the other samples.

Lampanyctus niger (Figure 2)

This species, one of three forms of the *L. niger*-complex which occur near Hawaii, has minute pectoral fins and lower AO counts than the others; it was designated as "Form B" in Clarke (1973). Zahuranec[2] has recently identified the form as *L. niger* (sensu stricto). There was evidence from deep night tows taken during the same sampling period that a fraction of the population of *L. niger* did not vertically migrate; consequently, some of the day-caught specimens may not have ascended to the upper layers the previous night. (Such "non-migration" was also recorded in previous studies, see Clarke 1973.)

The *H*-test indicated no significant diel differences in stomach fullness ($P>0.10$), and none of the adjacent pairs differed significantly. The medians from nighttime show a trend similar to that of other myctophids, but the means were highest during the day. No specimens were available from SR. Values of stomach fullness were overall much lower than observed in other species. Stomach fullness exceeded 1% in only 21 of the 160 specimens, and over 50% of the stomachs were empty at all periods except N2, N3, and N4.

The most frequent food items were large copepods of the familes Metridiidae, Euchaetidae, and Aetideidae and small (<10-15 mm TL) euphausiids. Occasionally small fishes were found. Intact prey items were found in stomachs from all periods. Deep-living copepods such as *Metridia* and *Pseudochirella* were noted in day-caught specimens indicating that at least some feeding occurs during the day.

[2]B. J. Zahuranec. Oceanic Biology Program, Office of Naval Research, Arlington, VA 22217. Personal communications, June 1977.

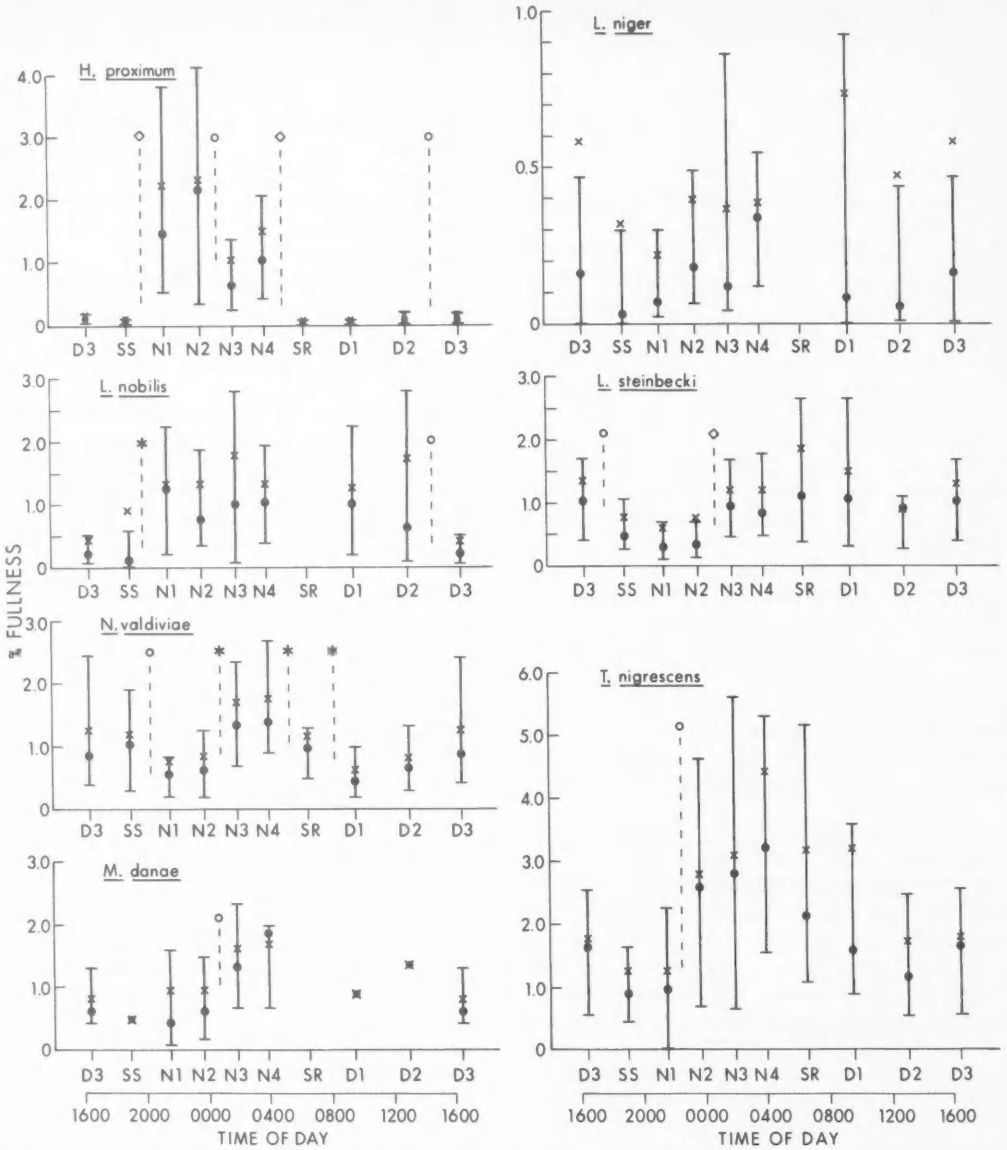

FIGURE 2.—Stomach fullness throughout the diel cycle for six species of myctophids and one species of melamphaid: *Hygophum proximum*, *Lampanyctus niger*, *Lampanyctus nobilis*, *Lampanyctus steinbecki*, *Notolychnus valdiviae*, *Triphoturus nigrescens*, and *Melamphaes danae*. Symbols and format as in Figure 1.

Lampanyctus nobilis (Figure 2)

Lampanyctus nobilis appeared to regurgitate food more frequently than other species examined. Because few specimens of *L. nobilis* were collected (none from SR and <20 from four other periods), I included in the analyses data from 19 specimens that had some partially digested food in the mouth

or esophagus. In all of these specimens, the stomach also contained food and was not everted; the remains from the esophagus or mouth were picked out as carefully as possible and added to the stomach contents. (No specimens with everted stomachs were included.) Use of these 19 specimens had the desirable effect of increasing the numbers upon which statistical estimates were based, but, as pointed out earlier, possibly biased the data because some of the regurgitated food may not have been recovered. The data were treated with and without these 19 specimens. Inclusion of the latter either had no effect or increased the significance of differences indicated without them. Thus bias, if any, that was introduced was insufficient to obscure between-period differences in stomach fullness.

Diel differences in stomach fullness were significant ($P<0.05$) and resembled the trends of other myctophids. There was, however, no clear indication of a peak value at dawn; no specimens from SR were available and the medians for N3, N4, and D1 were similar to each other. The percentage of empty stomachs was low throughout most of the night and increased steadily between D1 and SS.

The size-frequency distribution of the specimens was bimodal; 45% were <40 mm SL and 47% >60 mm. The small specimens had eaten mostly copepods and amphipods 1-3 mm and *Euphausia* spp. <10 mm, while the large ones ha ' taken large copepods (>3 mm PL) and euphausiids, mysids, sergestiids, and fishes 10-30 mm long. Intact prey were found frequently in night specimens and occasionally in those caught by day. The latter were, with the exception of a single *Lophothrix humilifrons* (apparently a deep-living copepod), migrating species that could have been taken at night. One specimen from N4 contained; among the remains of a euphausiid, crab megalopa, and copepods; a partially digested insect (probably a hymenopteran).

Lampanyctus steinbecki (Figure 2)

Stomach fullness values for *L. steinbecki* differed significantly ($P<0.005$) over the diel cycle. The medians generally increased from SS to SR and thereafter stayed at about 1% until a sharp decrease between D3 and N1. The percentage of fish with empty stomachs was low for all periods. The principal prey of *L. steinbecki* were copepods > ca. 2 mm PL—mostly aetideids, *Pleuromamma*, and *Candacia*—and euphausiids. A few intact items were found in specimens from D1 and D2 but all were shallow-living or migrating species that could have been taken the previous night. With the exception of a single *Pareuchaeta* sp. (probably a deep-living nonmigrator), the prey from D3 and SS were all well digested.

Notolychnus valdiviae (Figure 2)

The *H*-test indicated highly significant ($P<0.005$) diel differences in stomach fullness for *N. valdiviae*. Median values were low early in the night and increased to a peak at N4. The minimum value at D1 was slightly below the early night values. Stomach fullness increased slightly until SS and then decreased at SS-N1. The percentage of fish with empty stomachs was low at all periods. The positions of the 75th percentiles indicated higher percentages of fish with relatively full stomachs at N3, N4, SS, and D3.

Notolychnus valdiviae had taken a wide variety of sizes (ca. 0.5-4.0 mm PL) and species of copepods, but the bulk of the food in terms of weight was made up by large (relative to the weight of *N. valdiviae)* items such as *Pleuromamma xiphias, Candacia longimana,* and 2-4 mm aetideids. Intact prey were more frequently noted in specimens from N3 and N4 than in those from the apparent "secondary peak" in stomach fullness at D3 and SS. Considering only those specimens with stomach fullness >2% (whose numbers distinguish the peak periods from others), only three of the nine from D3 and SS contained intact or partially intact *Pleuromamma.* The other six contained remains that were either unrecognizable or barely so. In contrast, of the 15 specimens from N3 and N4, 12 contained 1-3 intact items, while only 3 contained unrecognizable remains. This plus the absence of any apparent significant differences associated with the D3/SS peak indicate that the latter was due to a chance collection of a few more specimens that had taken large meals the previous night rather than to extensive daytime feeding.

Triphoturus nigrescens (Figure 2)

Overall diel differences in stomach fullness were highly significant ($P<0.005$). Both medians and means rose from low values at SS and N1 to a peak at N4 and then, except for a slight increase at D3, declined until SS. Due to the broad overlap in

ranges and percentiles for most pairs, only the large increase between N1 and N2 was even marginally significant. The percentage of empty stomachs was highest at N1 and zero at and just after the peak at N4.

Triphoturus nigrescens fed principally on *Pleuromamma* and *Euphausia* spp. Intact prey were recorded more frequently during N2-N4 than in other periods. As in the case of *N. valdiviae*, the apparent peak at D3 was due to a few fishes' containing large amounts of well-digested material rather than freshly taken items.

Melamphaidae

Melamphaes danae (Figure 2)

Few *M. danae* were taken at any period. None were taken at SR, and only two or three were taken at SS, D1, and D2. The data indicate a diel trend similar to that of several myctophids, but the H-test indicated that diel differences were only marginally significant (P = ca. 0.10). If the data from SS, D1, and D2 were not included, the H-test indicated significance at P = ca. 0.05 and the N4 and D3 values differed at $P<0.05$. This latter, and statistically dubious, manipulation indicates that the apparent trend in the data is real, but that more specimens would be needed to confirm it properly.

Melamphaes danae fed on a wide variety of zooplankton including polychaetes and chaetognaths as well as crustaceans—mostly small copepods and ostracods. The copepods identified were all either vertical migrators or shallow-living, nonmigrating species. Intact items were present in nighttime specimens; those from daytime contained remains barely identifiable to general taxon.

Gonostomatidae

Gonostoma atlanticum (Figure 3)

Relatively few *G. atlanticum* were available from four periods even though 23 additional specimens from the May 1974 collections were included. Still there were significant ($P<0.05$) differences in stomach fullness over the diel cycle. Median values rose steadily from SR to D3, remained at ca. 2% between D3 and N2, and then dropped sharply between N2 and N3. Though the median for N4 was slightly higher than that for either N3 or SR, the percentage of empty stomachs was highest at N4 and SR, indicating an overall trend for decrease during the late night.

Gonostoma atlanticum fed on large copepods—mostly *Pleuromamma xiphias, Candacia longimana,* and aetideids and scolecithricids of several genera—and small (<10-15 mm) euphausiids. Intact prey were found in stomachs from all periods, but were mostly from the period between D1 and N2. The majority of the contents from N3 and N4 were well digested.

Gonostoma elongatum (Figure 3)

Relatively few *G. elongatum* were available from three periods and the size range of individuals used was extremely broad (26-150 mm). There is evidence from past studies that fractions of the population occasionally do not migrate (Clarke 1974), but catches from deep night tows taken during the same sampling period did not clearly indicate whether or not this occurred during this study.

The H-test indicated marginally significant differences ($0.05<P<0.10$) in stomach fullness over the diel cycle, and there was no clear trend in any of the parameters. Medians for all periods except SR (only 8 specimens) and D3 (10 specimens) were <1%. The means were well above the medians for several periods due to a few fishes' having very full stomachs. *Gonostoma elongatum* fed on the same copepods and euphausiids noted for *G. atlanticum* and on ostracods, amphipods, small sergestiid shrimps, and fish as well. Fresh or intact items were noted most frequently in specimens from SR, D1, D3, and N1.

Photichthyidae

Vinciguerria nimbaria (Figure 3)

Although previous evidence (Clarke 1974) indicated that a fraction of the population of *V. nimbaria* does not always migrate, catches of deep night tows from the same cruise indicated that only an insubstantial fraction, if any, remained at depth during the shallow night sampling periods.

Diel differences in stomach fullness were highly significant ($P<0.005$). The median was highest at SS and decreased steadily throughout the night to nearly zero at N4 and SR. The values were only slightly higher during the day, but increased sharply between D3 and SS. A clearer picture of changes between D2 and SS is given by the means

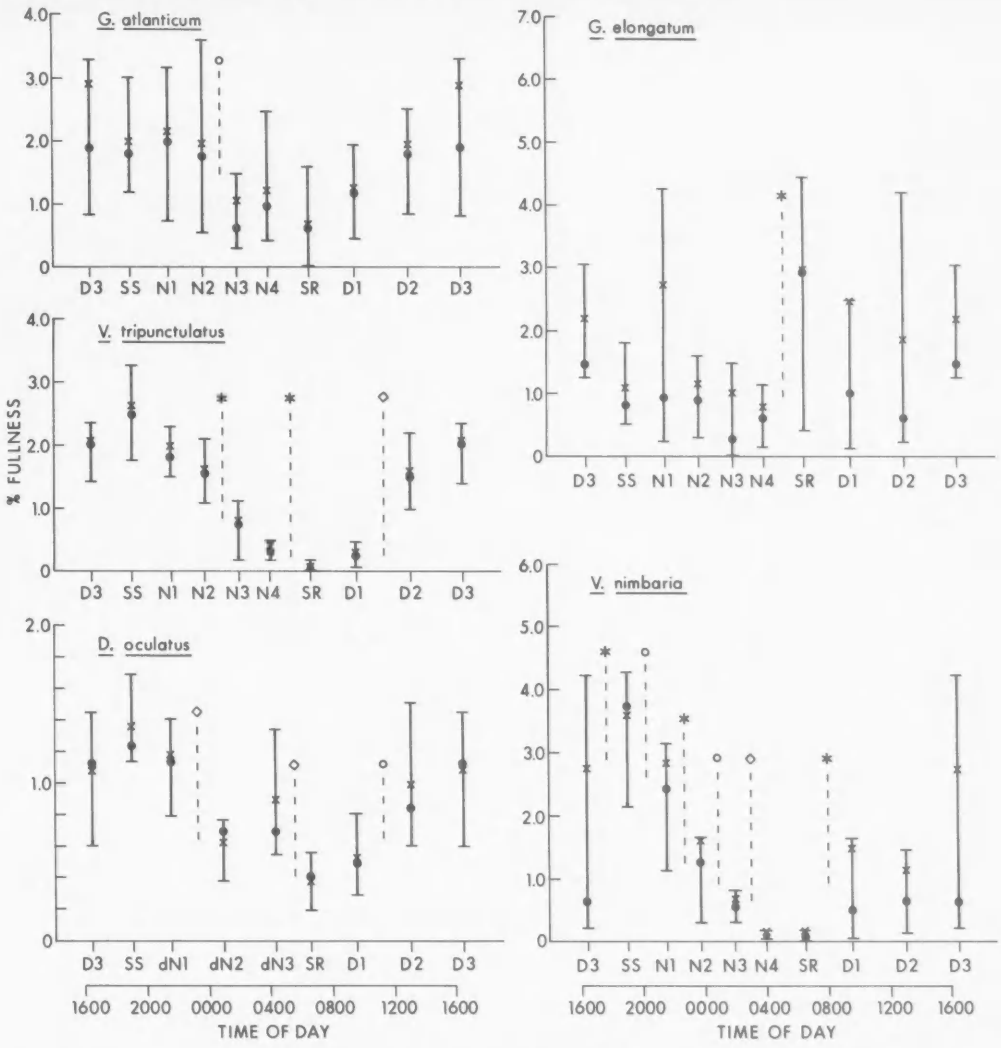
G. atlanticum
G. elongatum
V. tripunctulatus
V. nimbaria
D. oculatus
% FULLNESS
D3 SS N1 N2 N3 N4 SR D1 D2 D3
D3 SS dN1 dN2 dN3 SR D1 D2 D3
1600 2000 0000 0400 0800 1200 1600
TIME OF DAY

FIGURE 3.—Stomach fullness throughout the diel cycle for five species of stomiatoids: *Gonostoma atlanticum*, *Gonostoma elongatum*, *Valenciennellus tripunctulatus*, *Danaphos oculatus*, and *Vinciguerria nimbaria*. Symbols and format as in Figure 1.

rather than the medians, because there were marked differences in frequency distribution for these periods—differences to which the median is not sensitive. At D2 the data were skewed to the left with most values <1% and very few full stomachs. At D3 the data were bimodal; 7 values were higher than the mean of ca. 2.75% and 11 <1%. By SS, the data were again unimodal and skewed slightly to the right with 16 values >2% and only 2 <1%. Thus the trend between D2 and SS was one of a gradual change in percentages of the fish with very full stomachs, and the abrupt increase in median values between D3 and SS occurred as the high values became the dominant mode. The percentages of empty stomachs showed a trend opposite to that of the average values, i.e., an increase during the night and a decrease between SR and D2.

Vinciguerria nimbaria fed upon a wide variety of sizes and taxa of prey. Small (< ca. 2 mm PL) copepods and ostracods were most frequent, but larger copepods and small euphausiids occurred regularly. Both the number of prey items and absolute values of stomach fullness for the peak period were higher than for most of the the other species examined here; in several instances the remains of 20-40 prey items were found in a single stomach. Intact items were most frequent at SS and common in specimens from day samples. Some intact items were noted from N1 and a few from N2, but stomachs from N3, N4, and SR contained practically nothing but well-digested remains.

Sternoptychidae

Danaphos oculatus (Figure 3)

Few *D. oculatus* were available for any period except D1, and numbers were particularly low for D2. Nine of the specimens used came from the May 1974 series. In spite of this, there was an evident and highly significant ($P<0.005$) diel trend in stomach fullness. Median values rose steadily from a minimum at SR to a maximum at SS and declined nearly constantly throughout the night. There were a few empty stomachs at SR and D1 and none at other periods. *Danaphos oculatus* fed almost exclusively on *Pleuromamma xiphias, Euchaeta media*, and similar-sized juveniles and adults of several aetideid species. Intact items were most frequently noted in D3 and SS specimens; some were found in those from D1 and D2. Almost none of the night specimens contained any but well-digested remains.

Valenciennellus tripunctulatus (Figure 3)

Few *V. tripunctulatus* were available from any period except N1; 31 of the total examined came from the May 1974 collections. Still, like *D. oculatus, V. tripunctulatus* showed a clear and highly significant ($P<0.005$) diel trend in stomach fullness. Medians rose from zero at SR to a maximum at SS and declined throughout the night. The principal prey items were *P. xiphias, P. abdominalis, E. media*, and similar-sized aetideids. The stomachs from D2 to SS were nearly uniformly packed with intact prey while those from late night and SR were either empty or contained only traces of well-digested remains.

DISCUSSION

Feeding Chronology

Interpretation of data on stomach fullness is limited because observed fullness is a function of two rate processes—feeding rate and stomach evacuation rate. Diel changes in stomach fullness indicate that one or both rates vary over the diel cycle, but without independent estimates of one or the other, the only certain statements that can be made are that feeding exceeds evacuation during periods when fullness increases, the opposite when fullness decreases, and that both rates are zero when the stomach is empty. Notes on state of digestion of stomach contents are helpful, but must be interpreted with caution. Absence of intact items indicates that feeding rate is zero, but presence of intact items does not necessarily mean feeding rate was positive during a given period since some items may remain intact for an unknown time after feeding ceases. Still, it is possible within these limits to qualitatively consider changes in the two rates and to relate them to environmental changes which the fishes encounter over the diel cycle.

The species considered here undergo diel changes in numerous environmental factors, some of which are likely to affect either feeding or stomach evacuation rate in a qualitatively predictable manner. The migrating species encounter higher temperatures at night. Diel temperature changes for each species (Table 3) were determined using temperature-depth profiles from the study area (Maynard et al. 1975 give profiles from several seasons of three different years) and depth ranges of the fishes (Clarke 1973, 1974; Clarke and Wagner 1976). Because all species considered occur below the steepest part of the thermocline during the day, the magnitude of the diel temperature change is mostly a function of nighttime depth range and not day depth or absolute range of migration. For the same reason, juveniles, which occur shallower than adults in most species (Clarke 1973), incur greater temperature change than adults of the same species. The migrating species also encounter lower pressures and higher oxygen concentrations at night (oxygen-depth profiles for a site near the study area are given in Gordon 1970).

Unless the fishes are able to regulate metabolism over the range of diel changes, the day-night

TABLE 3.—Depth ranges, estimated diel changes in temperature, and probable day-night differences in prey concentration for the 16 species of fishes considered. (See text for sources of estimates.)

Species	Depth range (m) Night / Day	Temperature change (°C) Night-day	Prey density Night vs. day
Benthosema suborbitale	0-100 / 500-600	18-19	N>D
Bolinichthys longipes	50-150 / 500-700	16-19	N>D
Ceratoscopelus warmingi	0-150 / 600-1,000	16-20	N>>D
Diaphus schmidti	0-75 / 500-600	17-19	N>D
Hygophum proximum	0-150 / 500-700	15-19	N>D
Lampanyctus steinbecki	75-200 / 600-1,000	10-17	N>>D
Lampanyctus nobilis	50-150 / 600-1,200	16-20	N>>D
Notolychnus valdiviae	80-150 / 500-650	15-16	N>D
Triphoturus nigrescens	25-100 / 550-750	17-19	N>D
Melamphaes danae	75-200 / 750-1,200	10-18	N>>D
Danaphos oculatus	450-650 / 450-650	0	N<<D
Valenciennellus tripunctulatus	200-330 / 400-500	5-6	N<D
Gonostoma atlanticum	150-300 / 500-550	6-14	N≤D
Vinciguerria nimbaria	0-125 / 400-560	13-17	N≥D
Gonostoma elongatum	60-265 / 550-725	10-19	N≥D
Lampanyctus niger	100-300 / 650-900	7-15	N>D

differences in temperature and oxygen concentration both predict lower rates of metabolic processes in general and in particular lower feeding or stomach evacuation rate during the day. Childress (1975) and Childress and Nygaard (1973) indicated that mesopelagic organisms can regulate over a wider range of oxygen partial pressures than these fishes encounter off Hawaii. Thus temperature changes are more likely to affect rate processes. Teal (1971) showed that increased pressure can stimulate metabolic rates and thus mediate or cancel effects of temperature; however, it seems likely that temperature effects are predominant for the species considered here since these fishes migrate through a much stronger thermocline than did the shrimps studied by Teal.

As a consequence of vertical migration—by the fishes and by many of their prey—the fishes encounter diel differences in prey concentration, with which feeding rate is likely to be positively correlated. As noted above, the depth distributions of all prey species in the study area are not known in detail; however, general, qualitative features were evident from the available plankton samples (see above). Most of the important prey species were either shallow-living nonmigrators that occurred above ca. 200 m day and night or were vertical migrators with maximal concentrations at ca. 300-450 m by day. Some important genera, e.g. *Euphausia, Pleuromamma,* and *Euchaeta,* occurred as deep as 600 m during the day but not at high densities. At night, most copepods and many of the euphausiids occurred at highest densities above ca. 150-200 m. Many prey species occurred between 200 and 300 m at night, but except for a few euphausiid species, concentrations were much lower than in the upper 200 m. Below ca. 600 m by day and below ca. 300 m at night, total zooplankton concentration was low and that of important prey species nearly zero. Based on the above features and the fishes' depth ranges, qualitative estimates of day-night differences in prey concentration were made for each species (Table 3).

Nine species of myctophids and probably *Melamphaes danae* had similar diel patterns in that median values of stomach fullness were minimal at or near dusk and increased only at night, but details of the patterns were variable. Six species, *Benthosema suborbitale, Bolinichthys longipes, Ceratoscopelus warmingi, Diaphus schmidti, Lampanyctus steinbecki,* and *L. nobilis* (Figures 1, 2), had two periods of increasing stomach fullness during the night separated by a decline. Maximum stomach fullness occurred at or near dawn, and the fish reached day depth with relatively full stomachs. Stomach fullness appeared to decrease during the day in some species and showed no clear trend in others, but in most there was a significant decrease at or near dusk. In *Notolychnus valdiviae, Triphoturus nigrescens,* and possibly *Melamphaes danae* (Figure 2), median stomach fullness appeared to increase steadily throughout the night to a peak value just before dawn. In the first two of these species, stomachs were partially evacuated by the time they reached day depth. In *Hygophum proximum* (Figure 2) median fullness reached a peak value early in the night, and stomachs were completely evacuated by dawn.

For most of the above species there was no evidence of significant feeding at depth during the day. Intact items were more frequent at night, and stomach contents of day-caught fish were usually

well digested. *Lampanyctus nobilis* and *L. steinbecki* occasionally take deep-living copepods during the day, and *C. warmingi* apparently takes large items whenever it encounters them. Still, the instances of definite day feeding were so few in even the latter three species that the medians and, therefore the diel patterns, were only marginally affected.

All of these myctophids undergo diel changes in temperature and prey concentration (Table 3) that correlate with the observed pattern of feeding solely or mostly at night while in the upper 200 m. All are at much higher temperatures at night. Although some species occur as shallow as ca. 500-600 m during the day and thus partially overlap the daytime depth ranges of certain of their prey, all occur below daytime maxima of prey concentrations and almost certainly encounter higher concentrations at night. Certain details of the patterns of stomach fullness indirectly indicate that stomach evacuation rate may be lower during the day as predicted by temperature differences. In many species, stomach fullness did not clearly decrease during the day; since feeding rate was apparently zero then, the evacuation rates must have been low or zero. The sharpest declines in stomach fullness occurred at or near dusk in most species, near dawn in *N. valdiviae* and *T. nigrescens*, and during the night in *H. proximum*—not during periods when the fishes remained within their day depth ranges. In all cases except *H. proximum*, however, something related to vertical migration itself, e.g., activity, could be responsible for the apparent increases in evacuation rates.

Four species of stomiatoids, *Gonostoma atlanticum*, *Danaphos oculatus*, *Valenciennellus tripunctulatus*, and *Vinciguerria nimbaria*, fed only during the day. The last three species occur somewhat shallower by day then do the myctophids and are consequently at or near depths of maximum concentration of their prey then. The upward migration of *V. nimbaria* is similar in extent to that of its prey. Thus this species encounters little or no diel change. *Danophos oculatus* does not migrate, and *Valenciennellus tripunctulatus* migrates less than do its prey. Consequently, both species occur below high concentrations of prey at night. The adults of *G. atlanticum* (as were most specimens used here) occur near the lower depth limits of most prey species both day and night, and the day-night difference is probably minor. Thus in these species, the day depth ranges, rather than the occurrence or upward extent of migration, seem more related to observed feeding pattern.

All four species feed at nearly the same, low temperature. Diel temperature change is zero for *D. oculatus*, and relatively small for *V. tripunctulatus* and large *G. atlanticum* because they penetrate only part way through the thermocline. *Vinciguerria nimbaria* undergoes a change similar to that of the myctophids. The temperature changes or lack thereof obviously have no effect on feeding periodicity; however, the steepness of the nighttime decline in stomach fullness seems roughly correlated with nighttime temperature indicating an effect on stomach evacuation rates. This trend is considered in more detail below.

Lampanyctus niger and *G. elongatum*, the two species which showed no diel pattern in stomach fullness, do not undergo large diel changes in either temperature or prey concentration in spite of the fact that they migrate. The large individuals of both species (as were all the *L. niger* and most *G. elongatum*) undergo a relatively small temperature change. Likewise, only the smallest juveniles of either species encounter markedly higher prey concentrations at night. The relatively low values of stomach fullness in both species and the presence of deep-living, nonmigrating zooplankton in *L. niger* indicate that these two species feed at a low rate whenever and wherever they encounter prey.

Relationship to Previous Studies

Comparison of the present results with those of previous studies is restricted because methodology in all cases was different from that of the present study and in many cases equivocal or probably not sensitive enough to discern diel trends or lack thereof. With the exception of the study by DeWitt and Cailliet (1972), appropriate statistical testing was not done, and it is impossible to do so from the published data.

The most directly comparable study is that by Holton (1967) on *Lampanyctus* (= *Triphoturus*) *mexicanus*. Using 10 fish from each of eight periods of the day, he determined dry weights, but for some unknown reason weighed the entire alimentary canal with the food. The minimal values observed, presumably from empty stomachs, indicate that his "% nutrition" values should be decreased by about 2.5-3 to make them roughly comparable to those of the present study. Though

the ranges and standard deviations of the data are broad relative to the differences in means, the diel trend in the latter is similar to that observed here for *H. proximum*, i.e., peak value was reached early in the evening and then dropped to low values and probably zero before the dawn descent.

Most previous studies have used visual estimates of fullness with a scale of 3-5 ranks. Because of the lack of "intercalibration" between investigators, only the rank for "empty" can be compared unequivocally, and it is not certain in what manner the ranks might correlate with percentages of the fishes' dry bodily weight. Finally the validity or absence of trends and details thereof are questionable because scales of only 0-3 or 0-4 are rather insensitive. (Had only visual estimates of fullness been used for the present study, only in a few cases, e.g., *H. proximum* or *Valenciennellus tripunctulatus*, would the diel trends have been obvious.)

Anderson's (1967) data on *T. mexicanus* indicate a peak in stomach fullness just before sunrise, but his data on degree of digestion indicate that fresh food items were most frequent between sunset and midnight. His data for *Bathylagus stilbius* (cardiac portion of the stomach only) indicate two separate periods of increasing fullness at night and the sharpest decrease prior to ascent at dusk. This pattern correlates with frequency of less-digested prey items and is very similar to that observed for several myctophids in this study.

Similar indices were used in the studies of four species of high latitude myctophids: *Benthosema glaciale* (Gjösaeter 1973) and *Stenobrachius leucopsarus, Diaphus theta,* and *Tarletonbeania crenularis* (Tyler and Pearcy 1975). Both studies examined large numbers of specimens from each of a few, very broad time periods. Their data indicated highest percentages of full or nearly full stomachs at night and highest percentages of low values during the day. The occurrence of some full stomachs during the day led Gjösaeter to conclude that diel variation in feeding was not great and Tyler and Pearcy to conclude that there was no evidence against diurnal feeding. Both studies noted a higher degree of digestion during the day. These results are, however, consistent with the possibility that like many of the myctophids in the present study, their species descended at dawn with full stomachs and did not evacuate them completely until the dusk ascent. The latter may well have not been detected in these studies due to the broad time periods used.

Data on myctophids from recent studies by Merrett and Roe (1974) and Baird et al. (1975) are consistent with nocturnal feeding but are equivocal to varying degrees due to low numbers of specimens, incomplete diel coverage, or methodology. Both studies based stomach fullness estimates on counts of identifiable prey items. Apparently, the presence of a single resistant part, e.g., a *Pleuromamma* button, was counted the same as an intact, whole individual of the same taxon. Because of this and the likelihood that some prey taxa or parts of prey are digested—and concomitantly rendered unrecognizable—at different rates (e.g., Pandian 1967; Gannon 1976), such counts seem to be insensitive or possibly biased estimates of gut fullness—especially so when the counts are used to back-calculate dry weight as done by Baird et al. Furthermore, neither study corrected the fullness estimate for fish weight, which (using standard length ranges given by these authors and assuming that weight is roughly porportional to the cube of the length) varied by factors of ca. 7-15 in the myctophids covered by Merrett and Roe and ca. 2.75 in *D. taaningi*, the species studied by Baird et al.

Merrett and Roe's data for *L. cuprarious* indicated peak fullness in the middle of the night and a decrease before the dawn descent—a pattern similar to that of *H. proximum*. Their data for *Lobianchia dolfleini* and *N. valdiviae* include no samples between dusk and near dawn, but show fuller stomachs at dawn. Data of Baird et al. for *D. taaningi* are also similar to that for *H. proximum*. The rise in fullness from empty or nearly empty stomachs in the afternoon to fairly high values in early evening is evident and based on 39 and 9 specimens, respectively; however, the subsequent decline is based on a single specimen from late night and 4 from just after dawn (1 which contained a fair amount of food).

Fewer stomiatoids have been examined elsewhere, but much of the data available is consistent with diurnal feeding. Perhaps the most convincing data (because of good diel coverage and numerous specimens) presented by Merrett and Roe (1974) is that for *Valenciennellus tripunctulatus*, which does not migrate in their study area. The pattern is clearly similar to that observed for the Hawaiian specimens. Hopkins and Baird (1977) cited their own unpublished data also indicating diurnal feeding for the same species. Merrett and Roe (1974) interpreted dusk peaks of numbers of items/nonempty stomach as

an indication of dusk feeding activity in two species of *Argyropelecus;* however, the data for *A. hemigymnus* seem to me more consistent with increasing stomach fullness throughout the day and a nighttime decline. Except for high dawn values (based on only three specimens from two tows), *A. aculeatus* shows a similar trend.

DeWitt and Cailliet (1972) found no diel trend in feeding of *Cyclothone signata,* but, based on fewer empty stomachs in fish caught in the upper part of the depth range, proposed that this species, although it does not undertake diel vertical migrations, may ascend irregularly to levels of higher prey concentration to feed. Their data also indicated that a deeper living species *C. acclinidens,* had a higher percentage of empty stomachs by day; as noted by the authors, the latter seems to defy any reasonable explanation.

Legand et al. (1972) considered feeding chronology of 14 species of mesopelagic fishes from the South Pacific. Though trends in stomach fullness of some species are similar to those noted here, e.g., that for *Triphoturus microchir* (which almost certainly = *T. nigrescens)* is very similar to that for *T. nigrescens* near Hawaii, a number of species show patterns quite different from those reported by either the present or other studies. Interpretation of the validity of such "exceptions" is difficult owing to the sparse presentation of Legand et al. Though total numbers of specimens are fairly high, it is not clear that they were equitably distributed among diel periods, from the same area, or from the same season, etc. The percent fullness values are obviously based on wet weights—an imprecise measurement, particularly for stomach contents—and it is not clear whether all fish and stomach contents were weighed or some sort of averaging or regression procedure was employed.

The feeding patterns shown by previous studies cannot be compared in detail with those presented here; however, there is general agreement in data on the two dominant groups of mesopelagic fishes. Myctophids feed mostly at night, while stomiatoids tend to feed by day. My interpretations indicate that near Hawaii, the differences are at least partially related to different diel relationships of the fishes to vertical distributions of their prey. Other interpretations are obviously possible, e.g., the feeding patterns may prove to be characteristic of the two taxa regardless of relationship to prey distribution. It would be of particular interest to investigate myctophids with vertical distribution patterns similar to those of the stomiatoids, i.e., with shallow day depth ranges at or near high daytime concentrations of zooplankton. (Certain *Myctophym* and *Diaphus* spp. from Hawaii meet this criterion [Clarke 1973], but were not captured in sufficient numbers to be included in this study.)

The diel feeding patterns of mesopelagic fishes could well be related to light rather than (or in addition to) temperature and prey concentration. No data on diel light changes near Hawaii are available; however, data of Kampa (1970) from a similar area of clear oceanic water in the North Atlantic show that during full moon the diel change in depths of relevant isolumes is of the order of 300-350 m. Even allowing for considerable differences in extinction coefficients between Hawaii and Kampa's study area, the diel change in isolumes at new moon (when the present samples were taken) off Hawaii is probably at least 300-350 m and could be as great as 500 m. The absolute diel change in depth for most of the myctophids is over 500 m while that for the 4 day-feeding stomiatoids is ca. 400 m or less (Table 3). Thus it is possible that feeding in both groups occurs when higher light levels are encountered—at night for the myctophids and by day for the stomiatoids.

Estimation of Rates

As mentioned previously, neither feeding rate nor stomach evacuation rate can be considered quantitatively without an independent estimate of the other. Because of the difficulty in keeping mesopelagic fishes alive for grazing or evacuation experiments, it will likely be a long time before independent estimates are available. For a few species considered here it is, however, possible to derive "quasi-independent" estimates of evacuation rate given certain plausible assumptions. These allow, with further assumptions, rough estimates of feeding rate and daily ration.

For any period where feeding rate is zero, changes in stomach fullness are due to evacuation alone, and, if temperature, pressure, etc., remain essentially constant during that period, the rate of evacuation can be assumed to be proportional to the amount of food in the stomach (Kjelson and Johnson 1976; Eggers 1977). The change in stomach fullness would then be described by:

$$dS/dt = -kS \text{ or } S_t = S_0 e^{-kt} \qquad (1)$$

where S is stomach fullness as percentage of fish weight; S_0 and S_t, the values at the beginning and end of a period of t hours; and k, the instantaneous evacuation rate in per hour.

For most of the species considered here, there is no extended period of decline in stomach fullness where the above assumptions are met, but a rough estimate of k is possible for *H. proximum* and three species of stomiatoids. *Hygophum proximum* apparently ceases feeding early in the night, and stomach fullness declines from N2 to SR under essentially constant conditions, i.e., the fish remain in the upper layers. Stomach fullness declines from SS to SR in *Vinciguerria nimbaria, Valenciennellus tripunctulatus,* and *Danaphos oculatus,* and except for relatively brief periods of migration in the first two species, they remain at the same temperature, etc., for this period.

The values of k for these four species were calculated by simply using the integral form of Equation (1) and the median values of S for the beginning and end of the periods mentioned above (Table 4). (Other fitting procedures, such as least square methods, require that a number of questionable statistical assumptions be made.) The values of k are inversely correlated with night depth and thus positively with temperature being lowest for *D. oculatus,* highest for *Vinciguerria nimbaria* and *H. proximum,* and intermediate for *Valencienellus tripunctulatus.*

For each of the four species, prey concentration and temperature, pressure, etc., were essentially constant throughout the period when feeding occurred (SS to N2 for *H. proximum* and SR to SS for the stomiatoids). It is not unreasonable to assume, as a first approximation, that feeding rate was constant during the periods of increasing stomach fullness. Changes in fullness would then be described by:

$$dS/dt = F - k'S \qquad (2)$$

where k' is the instantaneous evacuation rate during the period of feeding, and F is the feeding rate in percentage bodily weight per hour. Integrating and rearranging gives an equation for F in terms of k', the duration of the feeding period t' in hours, and median fullness at the beginning (S_0') and end (S_t') of the feeding period:

$$F = \frac{k'(S_t' \times S_0' e^{-k't'})}{1 - e^{-k't'}}. \qquad (3)$$

(In some cases, there were a few relatively high values of stomach fullness among the data for a given period; consequently, the feeding rate of some individuals may have been lowered due to satiation. Such values had little effect on the median, and thus the assumption of constant feeding rate is probably not seriously violated as long as medians are used in the calculations.)

Estimates of feeding rate and daily ration ($= Ft'$) were calculated (Table 4) using median values of stomach fullness at SR and SS as S_0' and S_t', respectively, for the stomiatoids and, similarly, SS and N2 for *H. proximum.* Since both *D. oculatus* and *H. proximum* feed at the same temperatures as those under which the instantaneous evacuation rates were estimated above, k' in Equation (3) was assumed equal to k calculated from Equation (1). The daytime or "feeding" temperatures of *Vinciguerria nimbaria* and *Valenciennellus tripunctulatus* are lower than those under which k was estimated from Equation (1). During the day both species occur at nearly the same temperature as does *D. oculatus* both day and night. Consequently, for each of the two migrating stomiatoids, two values of feeding rate and daily ration are given in Table 4—one calculated using

TABLE 4.—Estimates of instantaneous stomach evacuation rates, feeding rates, and daily rations for four species of mesopelagic fishes based on changes in median stomach fullness over the diel cycle. The first three columns give the sampling periods (Table 1) between which feeding rate was assumed to be zero, the duration of this interval (t), and the calculated instantaneous stomach evacuation rate (k). The last five columns give the sampling periods between which feeding rate was assumed constant and positive, the duration of this interval (t'), the instantaneous stomach evacuation rate assumed for the feeding periods (k'), and calculated feeding rate (F in % of bodily weight per hour) and daily ration ($R = Ft'$ in % of bodily weight per day). For both *Valenciennellus tripunctulatus* and *Vinciguerria nimbaria,* two values of k', F, and R are given: the higher values under the assumption of constant stomach evacuation rate night and day ($k' = k$), the lower under the assumption that stomach evacuation rate during the feeding period was lower and equal to that estimated for the nonmigrating, deep-living, *Danaphos oculatus.* See text for formulae and further explanation.

Species	Nonfeeding period	t (h)	k (h^{-1})	Feeding period	t' (h)	k' (h^{-1})	F (%/h)	R (%/d)
Hygophum proximum	N2-SR	6.8	-0.52	SS-N2	4.5	-0.52	1.26	5.7
Danaphos oculatus	SS-SR	11.3	-0.10	SR-SS	12.7	-0.10	0.15	1.9
Valenciennellus tripunctulatus	SS-N4	8.7	-0.22	SR-SS	12.7	-0.22	0.57	7.3
						-0.10	0.34	4.3
Vinciguerria nimbaria	SS-SR	11.3	-0.38	SR-SS	12.7	-0.38	1.42	18.1
						-0.10	0.51	6.5

$k' = k$ from Equation (1) and the other using $k' = 0.10$, the value for *D. oculatus*.

The estimated ration for *Vinciguerria nimbaria* seems inordinately high (18%) if k' is assumed equal to k, the nighttime estimate of evacuation rate. Such values have been estimated for very young, rapidly growing zooplanktonivorous fishes, e.g., *Alosa aestivalis* (Burbidge 1974) and *Oncorhynchus gorbuscha* (Parsons and LeBrasseur 1970). Data from Kjelson and Johnson's (1976) study of postlarval *Lagodon rhomboides* and *Leiostomus xanthurus* feeding rates on zooplankton yield estimates of daily ration of only 9.4 and 8.6%, respectively, in terms of wet weight (my calculations from their data). The estimated ration for *V. nimbaria* using the low value for k' and that for *H. proximum* lie within the range of values observed for larger individuals in the first two studies cited above and for *Morone chrysops* juveniles feeding on zooplankton (Wissing 1974). The daily ration of the California sardine, *Sardinops caerulea*, which is a larger zooplanktonivore, is apparently slightly lower; judged from Lasker's (1970) estimates of metabolic and growth requirements, the daily ration is probably about 3-4% (in terms of calories) for the sizes considered.

The above comparisons are admittedly stretched and ignore, among other things, possible differences due to environmental temperature, but the similarity of estimated daily rations of *H. proximum* and *V. nimbaria* to those of shallow-living planktonivores is not entirely unexpected. Childress and Nygaard (1973) have shown that the chemical composition of mesopelagic fishes which migrate to the upper layers at night is more similar to that of epipelagic species than to non-migrating, deep-living forms.

Differences between estimates for the three stomiatoids are correlated with the extent of vertical migration. Nighttime stomach evacuation rate is highest in *V. nimbaria*, lowest in *D. oculatus*, and intermediate in *Valenciennellus tripunctulatus*. Feeding rate and daily ration estimates show the same trend regardless of whether or not daytime stomach evacuation rates are assumed lower. The absolute values of stomach fullness at the end of the feeding period (Figure 3) are also highest in *Vinciguerria nimbaria* and lowest in *D. oculatus*. These trends indicate a possible adaptive value for the upward migrations of some stomiatoids. The higher temperatures encountered at night by migrators could allow processing of larger meals and presumably faster growth, turnover, etc., rates than for species which remain at depth day and night.

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ON THE RESTRUCTURING OF THE PELLA-TOMLINSON SYSTEM

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ABSTRACT

The time-dependent analysis of an earlier work is extended to the equilibrium case of the Pella-Tomlinson system, and the relationships between the equilibrium and nonequilibrium versions of the restructured system are developed. The dual formulations of the conventional analysis are avoided and maximum sustainable yield is separated from the indeterminacy of the system. All arbitrary coefficients are eliminated and the management components incorporated directly into the system equations. The source of the statistical degeneracy in the model is revealed and explicitly formulated, and in the companion article by D. Rivard and L. J. Bledsoe (this issue of the *Fishery Bulletin*) the restructured model is treated by a new statistical method that subdues the estimation failures associated with past treatments of the Pella-Tomlinson system.

Because the equilibrium versions of all stock-production models follow from steady-state integrations, the strategy of fishery regulation becomes a strategy of accommodation, so to speak, as determined by a pattern of balanced model states where removals just equal the productivities otherwise surplus to the maintenance needs of the stock. Population status usually enters the process in the simple, robust form of integrated numbers or biomass, and the removals of fishing constitute direct fractions of the whole fishable stock without reference to age or weight distributions. Since the appearance of Schaefer's work (Schaefer 1954) the strategy has been applied to the management of many fisheries. Schaefer devised a rational, linearized method for estimating the parameters of Graham's equilibrium model (Graham 1935) from the actual nonequilibrium yields and effort expenditures of a fishery, a contribution that is often misunderstood. In applying Schaefer's method or like schemes of synthesis, it is not so much that one hopes to observe a pattern of equilibrium levels in a fishery or even expects them to come about, but rather, by knowing the response history of a stock to various exploitation pressures, one might then be guided by the model in bringing a stock, through a sequence of management actions, into a state where some desired level of sustainable yield most likely abides. The philosophy is widely accepted in fisheries management but its application is often censured, either on economic or biological grounds (see, for example, Larkin 1977).

The exploitation model of Pella and Tomlinson (1969), as it is customarily thought of, extends the more "basic" model of Graham from a system of second degree in nonlinearity to a flexible or more "general" system of indeterminate degree. The increased flexibility comes into the Pella-Tomlinson model through the addition of a single exponential parameter, but the analytical peculiarities that accompany the improvement often lead to paradoxical ends since the equations of the system then permit the simultaneous generation of good data fits and poor parameter estimates (see the commentary of Ricker 1975:323-326 and the treatments of Fox 1971, 1975). This disturbing trait of the statistical model arises from the conflict between the variable (or parametric) curvature of the analytical model and the coupling of that curvature, in the conventional formulations, with all the coefficients of the system. As shown in a prior work (Fletcher 1978), those effects may be separated in the time-dependent analysis by restructuring the system equations so as to accommodate directly the critical-point coordinates of the system graphs. In this paper we extend the analysis to the equilibrium version of the Pella-Tomlinson system, and we show the relationships between the equilibrium model and the (restructured) time-dependent equations.

For a stock of mixed age classes, the most difficult problem in applying any equilibrium model will lie, essentially, in the interpretation of time-dependent transitions between idealized states (however momentary, long-enduring, or

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unobserved such states may be), since the stock will include simultaneously the young and the old, the older having accumulated a probabilistic history of mortality, fecundity, and growth which may differ considerably from the current schedule that affects both. Various tactics for adjusting the parametric mechanics of stock-production models to such long-term, delayed influences are given by Gulland (1969), Fox (1975), Walter,[2] and others, but in the case of the Pella-Tomlinson system the difficulties have been compounded by artifacts of the conventional analysis and by an instability inherent to the mathematical indeterminacy of the system itself. With the critical-point analysis, most of those impediments will convert to tractable relationships or vanish altogether. We can suppress the troublesome dual formulations associated with the conventional casting of the system, we can uncouple the indeterminate exponent and the coefficients of the governing equations, and we can make explicit the relationships between parametric graph curvature and the management components of the system.

THE REFORMULATED GOVERNING EQUATIONS

Stock-production models, as they are usually defined, arise from the common premise that a fish stock, when reduced by exploitation to a level below some prior abundance, will always strive to recover its former size in accord with some latent, self-regulating mechanism of restoration. Irrespective of the compensatory details, any such recovery must accrue directly from the productivity of the stock, and in the conventional representation of the Pella-Tomlinson system, the latent capacity for biomass production in a stock of fishes is given the dual formulation

$$\dot{P}(B) = \pm aB^n \mp b\,B, \qquad \begin{matrix}(1a)\\(1b)\end{matrix}$$

$\dot{P}(B)$ being the production rate of the stock at stock size B. Equation (1a) applies when exponent n falls on the range $0<n<1$, and Equation (1b) applies when $n>1$. In either case, all the critical components of the system—maximum stock size, maximum productivity, the stock level where maximum productivity occurs—depend in some way on the numerical value assigned to exponent n. That is, root B_∞ is given by

$$B_\infty = \left(\frac{a}{b}\right)^{1/1-n},$$

the critical ordinate p (which corresponds to the stock level where maximum productivity occurs) is determined by

$$p = \left(\frac{an}{b}\right)^{1/1-n},$$

while extremum coordinate m (which corresponds to productivity $\dot{P}_{max}$) must be determined from the formula

$$m = \pm \frac{b(1-n)}{n}\left(\frac{an}{b}\right)^{1/1-n},$$

the plus sign applying to Equation (1a) and the minus sign to Equation (1b).

Although exponent n controls the graph curvatures of Equations (1a) and (1b), the nonzero roots and extrema are controlled by B_∞ and the coordinate pair (p, m). As shown by Fletcher (1975), coordinate m has no essential dependence on exponent n, and with the appropriate transformations the dual formulation (Equations (1a, b)) may be suppressed. In consequence, either of the parametric sets $\{m, p, B_\infty\}$ or $\{m, n, B_\infty\}$ will constitute a complete set of independent governing parameters for latent productivity in the Pella-Tomlinson system, and the dual formulation (Equations (1a, b)) converts to the single differential equation for latent productivity

$$\dot{P} = \gamma m\left(\frac{B}{B_\infty}\right) - \gamma m\left(\frac{B}{B_\infty}\right)^n, \qquad (2)$$

with γ a purely numerical factor wholly prescribed by n as

$$\gamma = \frac{n^{n/n-1}}{n-1}. \qquad (3)$$

With the coefficients so cast, the sign reversals at turning point $n = 1$ become automatic, and the consolidated interval of definition for n becomes $0<n<\infty$ (the point $n = 1$ being a removable singularity). With parameter m thus separated from n in Equation (2), the undetermined exponent n can be defined solely by the ratio p/B_∞ in the relationship

[2]Walter, G. G. 1975. Non-equilibrium regulation of fisheries. Int. Comm. Northwest Atl. Fish. Res. Doc. 75/IX/131, 12 p.

$$\frac{p}{B_\infty} = n^{1/1-n}. \tag{4}$$

When n takes any value between zero and unity, coordinate p falls on the range between zero and B_∞/e; when n takes any value greater than unity, coordinate p falls on the range between B_∞/e and B_∞. Wherefore, with $\{m, p, B_\infty\}$ as the parametric set for Equation (2), p and B_∞ determine n; with $\{m, n, B_\infty\}$ as the parametric set, n and B_∞ determine p. In the complete exploitation model, maximum productivity m becomes maximum sustainable yield (MSY) and biomass level p becomes the equilibrium level (the "B_{opt}") where MSY occurs.

For any stock-production system, we may enter exploitation into the productivity formulation by the direct difference $\dot{P} - \dot{Y}$, with $\dot{Y}$ signifying the rate of biomass removal attributed to exploitation. Therefore, in writing

$$\dot{B} = \dot{P} - \dot{Y}, \tag{5}$$

we interpret $\dot{B}$ as being the resultant productivity that nets to the stock for its growth. When removal rate $\dot{Y}$ exceeds latent productivity $\dot{P}$, then net productivity $\dot{B} < 0$ and the stock declines; when $\dot{P}$ exceeds $\dot{Y}$, then $\dot{B} > 0$ and the stock increases. Should $\dot{Y} = \dot{P}$, then $\dot{B} = 0$ and biomass trajectory $B(t)$ exhibits an extremum, which is the necessary condition for equilibrium fishing. Yield rate $\dot{Y}$ customarily takes the form

$$\dot{Y}(t) = F(t) \cdot B(t) \tag{6}$$

with the assumption that all fish of the fishable stock share equal probabilities of capture. By admitting Equations (2) and (6) into Equation (5), the differential equation that governs net productivity in the restructured system becomes

$$\dot{B} = \gamma m \left(\frac{B}{B_\infty}\right) - \gamma m \left(\frac{B}{B_\infty}\right)^n - FB \tag{7}$$

and over any time interval, however brief, that mortality F might be presumed to have a fixed value, biomass variable B in Equations (6) and (7) has the general time-dependent solution

$$B(t) = \left({B_*}^{1-n} + C \exp\left((\gamma m/B_\infty - F)(1-n)\, t\right)\right)^{1/(1-n)}, \tag{8}$$

$$B_* = \left(\frac{\gamma m}{\gamma m - F B_\infty}\right)^{1/(1-n)} B_\infty.$$

With initial time t_0 set at zero, the integration constant C in Equation (8) becomes

$${B_0}^{1-n} - {B_*}^{1-n}.$$

The quantity B_*, when positive in Equation (8), becomes the adjustment level such that $B(t) \to B_*$ over time. When, for certain ranges of n and F, quantity $B_* < 0$, then the zero root of Equation (7) applies and $B(t) \to 0$. When mortality F takes the value

$$F_{MSY} \equiv \left(\frac{n-1}{n}\right) \frac{\gamma m}{B_\infty}, \tag{9}$$

irrespective of the value of parameter n, then $B(t) \to p$ and $\dot{Y} \to m$ (which are the conditions, in the equilibrium limit, for maximum sustainable yield). In terms of the parameter set $\{m, p, B_\infty\}$, Equation (9) becomes, simply,

$$F_{MSY} = \frac{m}{p}.$$

Figure 1 gives a summary of the general constraints on the time-dependent system; for a more detailed treatment of system behavior, see Fletcher (1978).

THE RESTRUCTURED EQUILIBRIUM SYSTEM

By Equations (2) and (5), the time-varying rate of yield in the reformulated Pella-Tomlinson system takes the form

$$\dot{Y} = \gamma m \left(\frac{B}{B_\infty}\right) - \gamma m \left(\frac{B}{B_\infty}\right)^n - \dot{B}, \tag{10}$$

and when, for given F and n, governing Equation (7) exhibits a positive root, then $B(t) \to B_*$ and $\dot{B} \to 0$ in Equation (10), and yield rate $\dot{Y}$, over sufficient time, approaches a constant value. In the steady-state (or "equilibrium") limit, yield then accumulates as

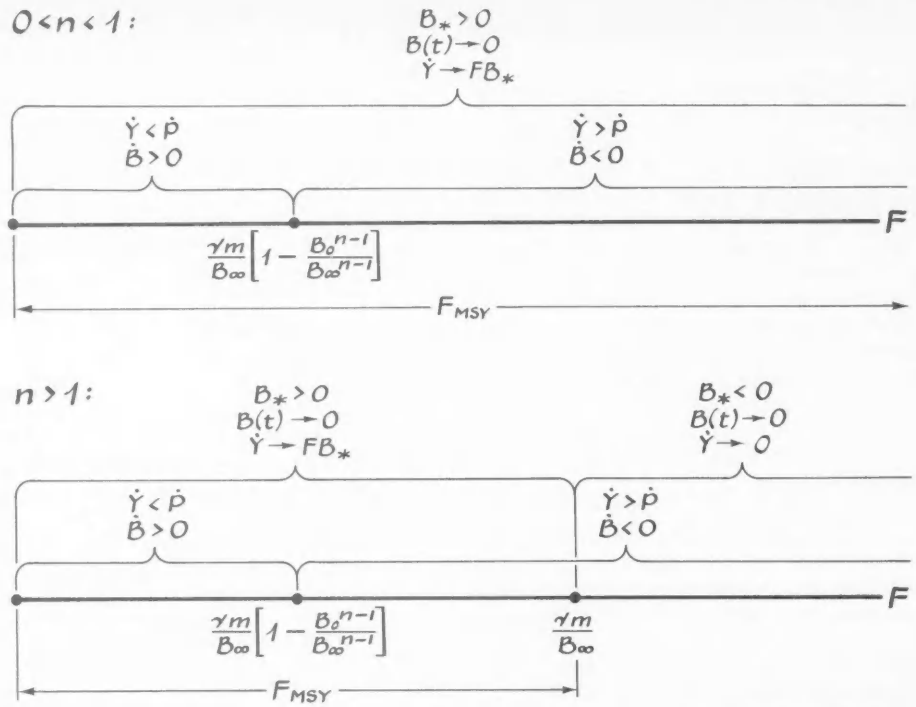


FIGURE 1.—Time-dependent response of the Pella-Tomlinson system to parametric variations of exponent n and mortality F. The upper diagram summarizes system response when n falls on the range $0 < n < 1$. The adjustment level of biomass is never zero for this range of n however great the value of F, and mortality F_{MSY} has no absolute constraints; such a stock cannot be fished to extinction. The lower diagram summarizes system behavior when n falls on the range $n > 1$. Mortality F_{MSY} is then constrained to the interval indicated by the diagram. When F exceeds the critical value $\gamma m/B_\infty$, then the stock, over sufficient time, trends to extinction.

$$\int dY = \int \left(\gamma m \left(\frac{B_*}{B_\infty} \right) - \gamma m \left(\frac{B_*}{B_\infty} \right)^n \right) dt - 0,$$

and for any such equilibrium interval τ, the integrated yield rate (Y_*/τ) takes on the parametric formulation

$$\frac{Y_*}{\tau} = \gamma m \left(\frac{B_*}{B_\infty} \right) - \gamma m \left(\frac{B_*}{B_\infty} \right)^n, \qquad (11)$$

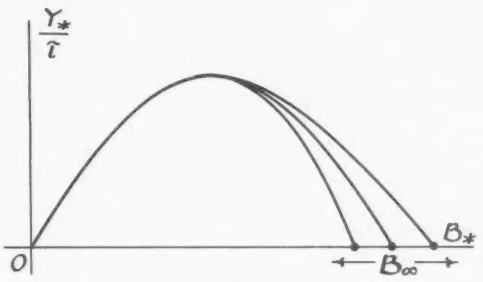
with maximum latent productivity m of the time-dependent system becoming the maximum sustainable yield rate (the MSY) of the equilibrium system. With B_* as the parametric variable in Equation (11), a zero left endpoint exists for Y_*/τ when $n > 1$ and $F = \gamma m/B_\infty$. Should F exceed the critical value $\gamma m/B_\infty$ when exponent $n > 1$, no equilibrium state exists; such conditions in the time-dependent system correspond to extinction trends. But when n has any value on the range $0 < n < 1$, no left endpoint of Equation (11) exists; a positive equilibrium level of biomass and a non-zero yield rate may be defined for any value of F, however great.

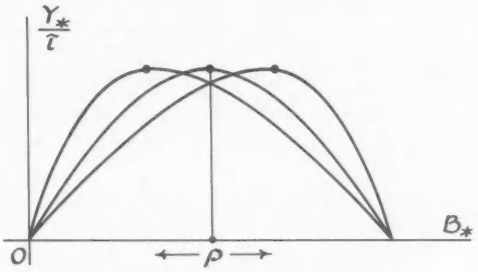
The equilibrium biomass level p where MSY (or m) occurs can be regulated in Equation (11) by relationship (4). And once designated in (4), the corresponding value of n determines the value of coefficient γ, as given by Equation (3). Either of the parametric sets $\{m, p, B_\infty\}$ or $\{m, n, B_\infty\}$ (augmented by the auxiliary parameters F and B_* or F and B_0) will constitute a complete, independent set of controls for equilibrium yield in the Pella-Tomlinson system. Collectively, the parameters control the behavior of equilibrium model Equation (11) but the influence of any one parameter remains independent of the remaining

two. Figure 2 illustrates the individual effects of set $\{m, p, B_\infty\}$ on the graph of Equation (11).

In equilibrium model (11), biomass level B_* varies parametrically as a function of equilibrium fishing mortality F. In terms of parameters m, n, B_∞, the relationship becomes

$$B_* = \left({B_\infty}^{n-1} - \frac{{B_\infty}^n}{\gamma m} F\right)^{\frac{1}{n-1}}. \qquad (12)$$





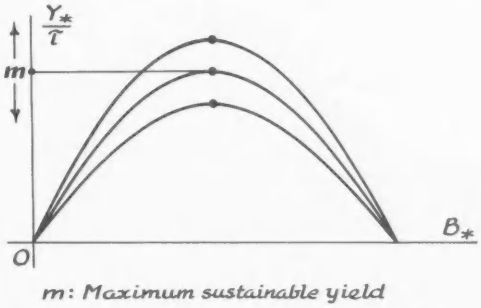


FIGURE 2.—The graph of Equation (11), equilibrium yield vs. equilibrium stock size in the Pella-Tomlinson system, as controlled by independent parameters m, p, B_∞.

When exponent n of the system takes any value on $0<n<1$ then $\gamma<0$, in which case we can see by Equation (12) that $B_*>0$ no matter how great the value of F. That is, when $0<n<1$ there exist equilibrium adjustment levels of stock biomass for all magnitudes of fishing mortality large and small; such a stock defies annihilation. Should exponent $n>1$, however, the corresponding stock can have nonzero adjustment levels B_* only when $F<\gamma m/B_\infty$. That is, when $n>1$ and when fishing mortality exceeds the critical value $\gamma m/B_\infty$, the "adjustment" level corresponds to extinction and Equation (12) does not apply.

Upon the substitution of Equation (12) into Equation (11), the direct relationship between equilibrium yield and equilibrium fishing mortality becomes

$$\frac{Y_*}{\tau} = \left(F^{n-1} - \frac{B_\infty}{\gamma m} F^n\right)^{\frac{1}{n-1}} B_\infty, \qquad (13)$$

and the fishing mortality that maximizes Equation (13) is given by Equation (9). That is, with the substitution of F_{MSY} into Equation (13) then $Y_*/\tau = m$.

Under the equilibrium conditions, the conventional quantity U (which signifies accumulated catch per unit of fishing effort as a function of fishing intensity f/τ) can be cast into the restructured form

$$U = \left({U_\infty}^{n-1} - \frac{{U_\infty}^n}{\gamma m} \frac{f}{\tau}\right)^{\frac{1}{n-1}}, \qquad (14)$$

which eliminates the explicit appearance of catchability coefficient q, permitting instead the direct quantification of maximum sustainable yield m. Quantities U and U_∞ have the customary meanings

$U \equiv \frac{Y_*}{f}$ (Y_* being the yield accumulated over time interval τ as a consequence of effort f).

$U_\infty \equiv qB_\infty$ (q being the individual probability of capture per unit of fishing effort f).

Should the accumulation interval τ be a year, the variable U becomes annual CPUE (catch per unit of effort) and the variable f/τ becomes effort per annum. With exponent $n>1$ in the Pella-Tomlinson system, no steady-state CPUE exists for a fishing intensity in excess of critical value $\gamma m/U_\infty$. But if n

has any value on the interval $0<n<1$, then steady-state CPUE will exist for all magnitudes of effort (save $f=\infty$). Trajectories of Equation (14) are similar to those of Equation (12), and any graph of (12) will represent the corresponding graph of (14) (CPUE as a function of fishing intensity) with the substitution of U for B_*, f/τ for F, and the ratio $\gamma m/U_\infty$ for $\gamma m/B_\infty$.

DISCUSSION

For all its adaptability, the Pella-Tomlinson system has serious, inherent limitations and it cannot be viewed as a perfectly generalized model of exploitation-productivity relationships. It is, instead, a nonlinear, first-order, wholly empirical system of open degree that admits of a convenient flexibility in a minimum number of terms. Properly regarded, a particularization of the system will accommodate an arbitrary prototype to the extent that the system graphs might be geometrically accommodating to the data.

Experience with the model has shown that unrealistic estimates of coefficients are likely to occur when the data lie in confined or badly scattered patterns over ranges of effort and yield. The tendency to unrealistic estimates arises from the conflict between graph curvature, as controlled by exponent n, and the coupling of n with the coefficients of the system. Heretofore, the exact relationships between exponent n and the management components have been obscured by the conventional casting of the system. But with the independent parameters and the restructured equations, much of the parametric uncertainty associated with previous statistical treatments can be circumvented. As we have seen, maximum sustainable yield m bears no essential relationship to exponent n, and m may be wholly separated from n in all the system equations. And despite the fact that parameters m, p, B_∞ share no interdependence (any one may be varied without change in the value of the others), the parametric ratio p/B_∞ determines n in the relationship (4). But n in turn prescribes the curvature (hence the fit) of every graph of the system. As indicated by Figure 3, exponent n exhibits a dismaying sensitivity to perturbations in ratio p/B_∞. The variational response in n, for a perturbation of 10^{-1} in p/B_∞, is of the order of n near $n = 1$, and the instability increases as $p/B_\infty \rightarrow 1$. Therefore, when an estimation procedure depends solely on a general curve-fitting statistic, poor parameter estimates are likely to follow, owing to stochastic displacement of datum points at biomass levels remote from locations p and B_∞. In the article that follows, Rivard and Bledsoe (1978) address such problems directly and their work illustrates certain advantages of the restructuring treated here.

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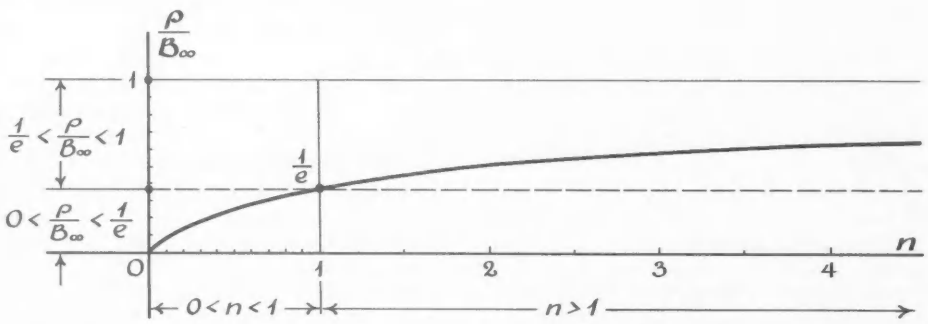

FIGURE 3.—Graph of the relationship between parameter ratio p/B_∞ and exponent n of the Pella-Tomlinson system, which indicates the slow convergence of the ratio for increasing n.

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PARAMETER ESTIMATION FOR THE PELLA-TOMLINSON STOCK PRODUCTION MODEL UNDER NONEQUILIBRIUM CONDITIONS

D. RIVARD AND L. J. BLEDSOE[1]

ABSTRACT

To estimate the parameters of the Pella-Tomlinson model, as restructured by Fletcher in this issue, we suggest a derivative-free version of the Levenberg-Marquardt algorithm, along with an algorithm that locates starting values for the iterative procedure. The iterative method of Levenberg-Marquardt was applied to two versions of the restructured model: five parameters were estimated in the first version and three in the second, the latter preventing degeneracy of the model to exponential form. We discuss in particular the causes of the degeneracies associated with previous applications of the model. Such faults lie, inherently, with the mathematical indeterminacy of the system equations themselves, so that all nonlinear estimation methods will tend to be inefficient in the absence of external constraints. The effectiveness of the Levenberg-Marquardt method was evaluated by Monte-Carlo simulation. As examples, we analyzed catch-effort data from the yellowfin tuna fishery of the eastern Pacific and catch-effort data from the Pacific halibut fishery (Area 2 of the International Pacific Halibut Commission).

Parameter estimation has been the greatest source of difficulty in applying the generalized stock-production model to management schemes, and the problem has attracted considerable attention. Pella and Tomlinson (1969) fitted the model to the catch-effort history of a fishery under nonequilibrium conditions by means of a search algorithm, and although good graphical fits are generally obtained by that procedure, unreasonable parameter estimates are frequently generated owing to the lack of internal constraints on parameter values (see Ricker 1975, example 13.6). Fox (1971) constructed a stochastic representation of the generalized production model and employed simulation to infer the effects of random variability in catch data. Fox suggested that variation in catch increases with the size of the catch (additive proportional error) and he gave a new formulation of the minimization criterion for the Pella-Tomlinson procedure. Walter (1975) suggested a graphical method for calculating the coefficients of the Graham-Schaefer model. Walter's procedure requires the plotting of catch per effort against effort data and then correcting for disequilibrium of the fishery. Fox (1975) also described a procedure for fitting the Pella-Tomlinson model that requires equilibrium approximations. And finally, Schnute (1977) derived linear and nonlinear methods for finding estimates of the coefficients of the Schaefer model; his method also includes a way of measuring the uncertainty of the estimates.

Fletcher (1978b) presented a reparametrization of the generalized production model and explains how the tendency to ill-determined parameter estimates arises from a conflict between variable graph curvature and its coupling with the coefficients of the system. In this paper, we take advantage of that restructuring and examine the use of a derivative-free version of the Levenberg-Marquardt numerical optimization algorithm, together with a Runge-Kutta differential equation solver, to estimate parameters in Fletcher's differential form of the Pella-Tomlinson model. Estimates of the variability in the coefficients are also provided, and the complete estimation procedure is analyzed by a Monte-Carlo simulation. The estimation problem is finally reformulated to prevent ill determination of the parameters and degeneracy of the model to exponential form.

MODEL AND NOTATION

As indicated by Fletcher (1975, 1978b), the generalized production model can be generated by the single differential equation

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$$\dot{B} = \gamma m \left[\frac{B}{B_\infty}\right] - \gamma m \left[\frac{B}{B_\infty}\right]^n - \dot{Y}, \qquad (1)$$

with the quantity γ wholly a function of n in the relationship

$$\gamma = \frac{n^{n/n-1}}{n-1}. \qquad (2)$$

$B(t)$, the solution of $\dot{B}$, represents the stock size at time t, while $Y(t)$, the solution of $\dot{Y}$, represents the cumulative catch of the stock. Parameter B_∞ is the maximum stock size of the unexploited population, while m is the maximum productivity in the productivity function or the maximum sustainable yield (MSY) in the complete exploitation model. Exponent n controls the location of the inflexion point in the latent productivity function of the stock. Therefore, parameters B_∞, m, and n are nonnegative. With this new formulation of the system equations, the sign reversals of the coefficients at the turning point $n = 1$ are now automatic. Also the parameters are expressed in more meaningful terms for the fishery scientist, and some aspects of parameter estimation are simplified thereby.

By presuming that $f(t)$ units of effort operate on the population over time increment dt, the yield rate is often put into the instantaneous form

$$\dot{Y} = q f(t) B(t) \qquad (3)$$

where q is the catchability coefficient. Equations (1) and (3) constitute a coupled system of nonlinear differential equations. The system, as it is formulated in Equations (1) and (3), represents the continuous-time model. In practice, though, for each finite time interval τ over which yield statistics are integrated, fishing effort is usually assumed to be constant. It follows that $f(t)$ must be a step function that describes the effort as being constant over each time interval τ with abrupt changes at the end of each period. Then the effort required, over one time interval, to maintain maximum productivity is given by

$$f_{\mathrm{MSY}} = \frac{\gamma m}{q B_\infty}\left[\frac{n-1}{n}\right], \qquad (4)$$

and at MSY the yield per unit of effort U_{MSY} is obtained by dividing m by f_{MSY}.

DETERMINISTIC MODEL AND STOCHASTIC REPLICATES

The Pella-Tomlinson system has the five parameters m, B_∞, n, q, and B_0. The fifth parameter, initial population size B_0, is needed to specify a particular solution of Equation (1). By taking the following arbitrary values for the parameters,

$$m = 1.36 \times 10^6 \qquad q = 4.60 \times 10^{-6}$$
$$B_\infty = 3.48 \times 10^6 \qquad B_0 = 3.48 \times 10^6$$
$$n = 1.80,$$

we constructed an example of a fishery over the course of 20 yr with $f(t)$ increasing within the first 10 yr and stabilizing thereafter (Table 1).

We also constructed 20 stochastic replicates of the deterministic catch history. In all the stochastic versions we assume additive proportional error terms ϵ_i (with i the annual index), consisting of 20 sets of 20 values each of normally distributed, independent random variables with expected means of zero and standard deviations (σ) of 0.025, 0.050, 0.075, 0.100, 0.125, 0.150, 0.175, 0.200 (12 replicates), and 0.250. Although Fox (1975) takes a similar approach, we recognize the fact that serial correlation of errors is likely to exist in natural data. As put by J. J. Pella in a personal communication, "If yield is above average in one year because the population is above average, it will probably be above average in the following year." But at this stage of the analysis, the explicit consideration of serially correlated errors would only complicate the estimation problem unneces-

TABLE 1.—Simulation of a logistic stock under exploitation (deterministic model).

Time (yr)	Catch	Effort	$U = \frac{\text{Catch}}{\text{Effort}}$
1	79,529	5,000	15.91
2	156,989	10,000	15.70
3	306,812	20,000	15.34
4	516,722	35,000	14.76
5	893,564	65,000	13.75
6	1,129,740	90,000	12.55
7	1,402,830	125,000	11.22
8	1,565,040	160,000	9.78
9	1,631,400	195,000	8.37
10	1,614,130	230,000	7.02
11	1,478,930	250,000	5.92
12	1,434,220	300,000	4.78
13	1,196,850	320,000	3.74
14	988,745	320,000	3.09
15	895,127	350,000	2.56
16	737,908	350,000	2.11
17	607,937	300,000	2.03
18	649,627	300,000	2.17
19	632,633	250,000	2.53
20	773,600	250,000	3.09

sarily; our immediate purposes are better served by the simpler form of the ϵ_i. We want to observe the response of the estimation procedure to realistic levels of stochastic error, but we also want to avoid wrong interpretations in those cases where parameter values might be ill determined because of some inherent fault of the estimation procedure itself and not because of some complication of the error structure. Therefore, the stochastic replicates, as well as the objective function of our estimation procedure, are constructed on the assumption of independence of errors. As we shall see in a subsequent discussion, the following estimation procedure is indeed robust with respect to that assumption.

PARAMETER ESTIMATION PROCEDURE

In its general form, the solution of the nonlinear model described by Equation (3) can be written as

$$\hat{Y}_i = g(f_1, f_2, \ldots, f_i; \boldsymbol{\Theta}) \quad i = 1, 2, \ldots, r \qquad (5)$$

where[2] $\boldsymbol{\Theta} = [m, B_\infty, n, q, B_0]^T$.

Quantity r represents the total number of observations over time, f_i the fishing effort during time interval i, and $\hat{Y}_i$ the predicted yield (biomass or number) over the interval i. Following Fox (1971), we also consider an error term ϵ_i proportional to population size and equivalent in terms of yield to the form

$$Y_i = \hat{Y}_i + \hat{Y}_i \epsilon_i, \qquad (6)$$

where Y_i represents the observed yield over the interval i. Then the error is described by the relationship

$$\epsilon_i = (Y_i - \hat{Y}_i) / \hat{Y}_i. \qquad (7)$$

Least squares estimation of $\boldsymbol{\Theta}$ by a vector $\hat{\boldsymbol{\Theta}}$ requires minimization of the function

$$S(\hat{\boldsymbol{\Theta}}) = \sum_i \epsilon_i^2. \qquad (8)$$

In terms of residuals $(Y_i - \hat{Y}_i)$, this is equivalent to

$$S(\hat{\boldsymbol{\Theta}}) = \sum_i W_i (Y_i - g(f_1, \ldots, f_i; \hat{\boldsymbol{\Theta}}))^2, \qquad (9)$$

where the W_i are statistical weights. That is, from Equation (7),

$$W_i = \hat{Y}_i^{-2}. \qquad (10)$$

If $S(\hat{\boldsymbol{\Theta}})$ were an analytic form, we would find $\hat{\boldsymbol{\Theta}}$ by writing the normal equations

$$\left[\frac{\partial S(\hat{\boldsymbol{\Theta}})}{\partial \Theta_i}\right] = 0.$$

Since S must be calculated via numerical methods, we will instead consider $S(\hat{\boldsymbol{\Theta}})$ as a continuous function that describes a hypersurface in a five-dimensional parameter space; that space must be searched for the appropriate minimum value of $S(\hat{\boldsymbol{\Theta}})$. The iterative process of successive approximations which we employ is an adaptation of the Levenberg-Marquardt technique (Levenberg 1944; Marquardt 1963). Given some initial estimate $\boldsymbol{\Theta}_0$, the method generates a sequence of estimates $\hat{\boldsymbol{\Theta}}_j$ from the inductive relation

$$\hat{\boldsymbol{\Theta}}_{j+1} = \hat{\boldsymbol{\Theta}}_j - \left[\beta_j \mathbf{I}_5 + \mathbf{J}_j^T \mathbf{J}_j\right]^{-1} \mathbf{J}_j^T \epsilon_j. \qquad (11)$$

In Equation (11), β_j is a positive constant, $\mathbf{I}_5$ the identity matrix of order 5, $\mathbf{J}_j$ an r by five matrix having elements $\partial \epsilon_i / \partial \hat{\theta}_k$ $(i = 1, \ldots, r; k = 1, \ldots, 5)$, and ϵ_j the vector of errors after j iterations. The method combines the best festures of both the gradient and the Taylor series methods and avoids their most serious limitations (Conway et al. 1970). We employ a FORTRAN computer program which incorporates a derivative-free version of the Levenberg-Marquardt method (Brown and Dennis 1972), and we approximate the solution of the model differential equations (1) and (3) by a fourth order Runge-Kutta algorithm for numerical integration. The general structure of the program is shown by the flow diagram of Figure 1. Since all the parameters have to be positive, we also constrain the optimization by transforming each component of $\hat{\boldsymbol{\Theta}}$ by its absolute value before evaluating the model.

ACCURACY OF RESULTS

Since the solution to the least-squares estimation problem is the result of a numerical search along the $S(\hat{\boldsymbol{\Theta}})$ hypersurface, we do not generate

[2]The notation [. . .] indicates that a row vector or matrix is formed of the elements enclosed by brackets.

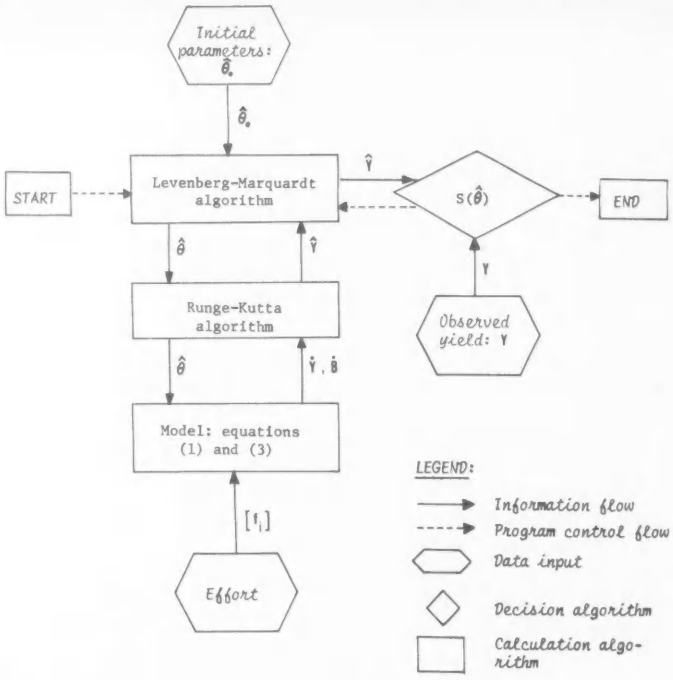

FIGURE 1.—Information flow diagram for the computer program written to estimate the coefficients of the generalized production model.

an analytical form for the uncertainties in the final values of the parameters (Bevington 1969). By letting $S(\hat{\mathbf{\Theta}})$ be the weighted residual sum of squares for the final parameter estimates, however, the variance-covariance matrix of the estimates (Bard 1974) can be approximated by

$$V_{\mathbf{\Theta}} = \left[\mathbf{J}^T \mathbf{J}\right]^{-1} S(\hat{\mathbf{\Theta}})/(r-5). \qquad (12)$$

Some idea of the joint variability of the parameters can be obtained by evaluating the ellipsoidal confidence region, based on the assumption that the linearized form has validity around $\hat{\mathbf{\Theta}}$ (Draper and Smith 1966). The confidence region is then given by

$$[\mathbf{\Theta}-\hat{\mathbf{\Theta}}]\ \mathbf{J}^T\ \mathbf{J}[\mathbf{\Theta}-\hat{\mathbf{\Theta}}]^T \leq \frac{5S(\hat{\mathbf{\Theta}})}{r-5}\ F(5, r-5, 1-\alpha), \qquad (13)$$

where $F(5, r\text{-}5, 1\text{-}\alpha)$ is the standard tabulated F-statistic. The ellipsoid is not a true confidence region, of course, since the dependent variable, $\dot{Y}$, is a nonlinear function of $\hat{\mathbf{\Theta}}$. The intervals obtained are valid to the extent that a linear approximation in the neighborhood of $\hat{\mathbf{\Theta}}$ is appropriate. A necessary and sufficient condition for the F-distribution to be appropriate here is that differences in true and estimated parameter values are independent and approximately normally distributed with zero mean and equal variance.

DETERMINATION OF STARTING VALUES

In order to reduce the number of iterations required to minimize Equation (8), reasonably accurate starting values should be employed. Starting values can be calculated from a linearization and simplification of the basic model.

STEP 1. By using $Y_1, Y_2, \ldots, Y_r$ and $f_1, f_2, \ldots f_r$, find an estimate of q from the Delury technique. Note that this procedure generally underestimates q (see Ricker 1975). Correction for q will be provided in step 4.

STEP 2. Find estimates of B_{t+1} from the equation

$$B_{t+1} = (\overline{B}_{t,t+1} + \overline{B}_{t+1,t+2})/2, \qquad (14)$$

where (by assuming $f_{t,t+1}$ constant over the interval $t,t+1$)

$$\bar{B}_{t,t+1} = Y_{t,t+1}/q\, f_{t,t+1}. \qquad (15)$$

Note that $Y_{t,t+1}$ and $f_{t,t+1}$ correspond to Y_i and f_i of Equations (6) and (5).

STEP 3. Let $n = 2$, as in the Graham-Schaefer model, and estimate m and B_∞ by fitting the linear model

$$y_t = \alpha_0 + \alpha_1 x_t, \qquad (16)$$

where $y_t = \dfrac{dB_t}{B_t\, dt} + qf_t, \quad x_t = B_t^{n-1},$

$$\alpha_0 = \gamma m/B_\infty, \quad \alpha_1 = \gamma m/B_\infty^n.$$

Equation (16) is derived from Equations (1) and (3). However, Equation (16) requires an estimate of the relative growth rate $dB_t/B_t dt$, say R_t. As suggested by Causton (1969), the mean value of R between t and $t+2$ is given by

$$\bar{R}_{t,t+2} = (\ln B_{t+2} - \ln B_t)/2. \qquad (17)$$

For the purpose of fitting Equation (16), quantity $\bar{R}_{t,t+2}$ may be considered an estimate of R_{t+1}, which corresponds to B_{t+1}. Whence. Equation (16) provides estimates of m and B_∞ as

$$m = \frac{\left[\alpha_1\, \alpha_0{}^n\right]^{(1/1-n)}}{\gamma}, \qquad (18)$$

$$B_\infty = \left[\frac{\alpha_1}{\alpha_0}\right]^{1/1-n}. \qquad (19)$$

STEP 4. Steps 2 and 3 are repeated iteratively for increasing values of q. The value of q which provides the minimum residual sum of squares $[\sum_i (Y_i - \hat{Y}_i)^2]$ is accepted as the appropriate starting value for q.

STEP 5. Step 3 is repeated iteratively for increasing values of n, parameter q being kept constant. The value of n which provides the minimum residual sum of squares $[\sum_i (Y_i - \hat{Y}_i)^2]$ is accepted as the appropriate starting value for n. In the last iteration, Equations (18) and (19) provide estimates of m and B_∞. Finally, B_0 is approximated by

$$B_0 = 2\bar{B}_{0,1} - B_1 \qquad (20)$$

where B_1 and $\bar{B}_{0,1}$ are estimated by Equations (14) and (15), respectively.

Steps 1 through 5 provide a set of starting values for the optimization algorithm (11). Usually the starting values are near the solution and few iterations will be needed. Of course, it would be possible to derive algorithms for more accurate starting values, but our purpose here is to find a rough estimate for each coefficient and to let the iterative procedure (11) converge to the minimum. Sometimes, by experience or by prior information, it is possible to provide starting values as satisfactory as those provided by the algorithm given above.

MONTE-CARLO SIMULATIONS

The parameter values that we chose to generate the data of Table 1 (deterministic model) were recovered exactly by the estimation procedure. Results of fitting 18 stochastic versions of the deterministic model are also included in Table 2. Based on our simulation results, there do not appear to be any serious problems with bias of parameter estimates. The bottom line of Table 2, which gives the coefficients of variation of the parameter estimates, reveals that estimates of the three parameters of principal interest to the manager have the smallest variability. Those parameters are maximum sustainable yield ($\hat{m}$, C.V. = 14%), optimal effort level ($\hat{f}_{MSY}$, C.V. = 6%), and yield per unit of effort at optimum effort ($\hat{U}_{MSY}$, C.V. = 9%). Our results confirm the observations of Fox (1971) and Pella and Tomlinson (1969) on the robustness of m and f_{MSY} with respect to error in the measurement of the yield data. From Table 2, we can also compare variance estimates from Equation (12) with variance of estimates for 10 replicates at $\sigma = 0.200$. Equation (12) appears to give (approximately) unbiased estimates of the variance of the sampling distribution of $\hat{\mathbf{\Theta}}$. Also, out of the 19 cases considered, the true parameter value lay outside the arbitrary ± 2 (SD) confidence interval twice for $\hat{m}$ and only once each for $\hat{B}_\infty$, $\hat{n}$, and $\hat{B}_0$. Although we did not employ an extensive Monte-Carlo simulation, our results suggest that the normal approximation to the sampling distribution of $\hat{\mathbf{\Theta}}$ is an acceptable approximation, at least for management purposes.

In a few additional simulations (replicates 13 and 15), parameters obtained by the five-parameter procedure were ill determined. A parameter is considered ill determined if its estimated value responds unreasonably to seemingly insignificant variations in the data (Bard 1974). The basic difficulty is that the model is extremely general and capable of several types of behavior over the space of $\boldsymbol{\Theta}$. In the Pella-Tomlinson system, ill determination often occurs whenever an iteration of the algorithm (11) gives an estimate of $\boldsymbol{\Theta}$ such that the point $(\hat{m}, \hat{f}_{MSY})$ of the yield-effort plane lies outside the concentration of data. In such a circumstance the exponent $\hat{n}$ takes on smaller and smaller values in the successive iterations and the solution of system (1) and (3) degenerates to an exponential form for which only four parameters are required for uniqueness. That is, as $n \to 0$, in Equation (1), then $(B/B_\infty)^n \to 1$ and $\gamma \to -1$. The five-parameter procedure then overprescribes the system, which in turn predisposes the coefficient estimates to extremely large variances. The ultimate irony here is the fact that wholly unrealistic parameter estimates still generate good fits to the catch-effort history (i.e. small residuals). For example, in Figure 2 the fitted five-parameter curve predicts f_{MSY} near infinity while in the true model f_{MSY} actually corresponds to 174,000 units of effort. However different the equilibrium curves are, the five-parameter procedure still generates a good fit to the catch history ($S(\hat{\boldsymbol{\Theta}}) = 1.10$). Incompleteness of information over a wide range of effort values, as well as excessive noise in the catch-effort data, will tend to bring about such pathological conditions.

To overcome these difficulties, reformulation of the estimation problem is necessary. By the following considerations, the five-dimensional parameter space can be reduced to three dimensions. First, we will approximate B_0 by Equation (20). Furthermore, if the data contain information on the yields under low exploitation, we may define B_∞ as

$$B_\infty = \text{MAX}(Y_i/q\, f_i) \quad i = 1, \ldots, r. \tag{21}$$

By using Equations (20) and (21), B_0 and B_∞ can be deleted from $\boldsymbol{\Theta}$, leaving only m, q, and n as the independent parameters requiring estimation. It is important to understand at this point that B_0 and B_∞ are not fixed; they are reevaluated by Equations (20) and (21) at each iteration, along with the parameters m, q, and n. In fact, the solution of Equations (1) and (3), as well as Equations (20) and (21), specify a new model with unknowns $\boldsymbol{\Theta} = [m, q, n]^T$. By this restructuring, much of the degeneracy associated with the model can be eliminated. As shown in Figure 2, this procedure also provides a closer correspondence between the "estimated" and the "true" equilibrium model. Furthermore, the three-parameter procedure still generates an adequate nonequilibrium catch history ($S(\hat{\boldsymbol{\Theta}}) = 1.40$). In a Monte-Carlo simulation study, parameter estimates obtained by using these transformations fell within reasonable

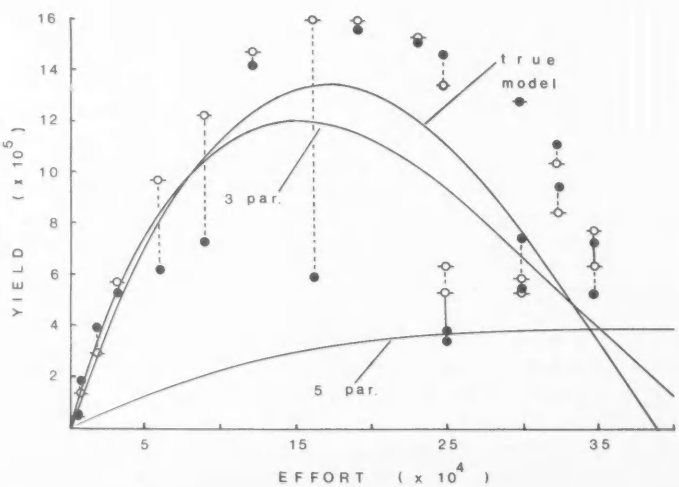

FIGURE 2.—Comparison of the "true" model with the models obtained by using the estimation procedure on three and five parameters respectively. Solid lines show equilibrium yield curves; data points show nonequilibrium simulated (dots) yields and predicted (circles) yield values from the three-parameter approach. Dashed vertical lines indicate the magnitude of residuals.

bounds (Table 3). Out of the 20 cases considered, the true parameter value lay outside the arbitrary ±2 (SD) confidence interval only once for $\hat{m}$ and $\hat{n}$. Also, variance estimates were comparable with the variance estimates of the five-parameter procedure (compare Tables 2 and 3).

TABLE 2.—Estimated parameters for the deterministic model and for 18 stochastic replicates. The Levenberg-Marquardt algorithm is employed in a five-dimensional parameter space (m, B_∞, n, q, B_0). For each parameter and replicate, the parameter estimate ± its estimated standard deviation from Equation (12) are tabulated. Replicates 13 and 15 have been excluded due to degeneracy of the model, as discussed in the text.

Replicate	σ	$\hat{\sigma}$[1]	$\hat{m}$ (10^6)	$\hat{B}_\infty$ (10^6)	$\hat{n}$	$\hat{q}$ (10^{-6})	$\hat{B}_0$ (10^6)	$\hat{f}_{MSY}$ (10^5)	$\hat{U}_{MSY}$
1	0.000	0.000	1.34±0.00	3.49±0.00	1.80±0.00	4.60±0.00	3.48±0.00	1.74	7.70
2	0.025	0.014	1.34±0.01	3.56±0.10	1.79±0.03	4.54±0.12	3.44±0.12	1.72	7.75
3	0.050	0.046	1.37±0.04	3.34±0.32	1.88±0.10	4.80±0.42	3.24±0.41	1.76	7.82
4	0.075	0.071	1.49±0.06	2.78±0.36	2.14±0.15	5.68±0.67	2.89±0.63	1.84	8.10
5	0.100	0.111	1.41±0.09	2.62±0.50	2.36±0.28	5.28±0.92	2.86±0.99	1.91	7.36
6	0.125	0.096	1.36±0.09	3.34±0.62	1.81±0.19	4.96±0.87	3.84±0.95	1.72	7.95
7	0.150	0.109	1.55±0.10	2.94±0.59	2.33±0.27	5.23±0.96	5.97±2.60	1.90	8.15
8	0.175	0.159	1.26±0.17	3.92±1.37	1.61±0.35	4.26±1.41	4.13±1.74	1.84	7.66
9	0.200	0.189	1.15±0.24	5.16±2.25	1.56±0.49	2.90±1.36	7.75±3.53	1.69	6.79
10	0.200	0.216	1.75±0.16	1.90±0.53	2.61±0.47	8.34±2.02	0.85±0.66	2.00	8.73
11	0.200	0.159	1.19±0.12	2.91±0.84	1.71±0.28	5.10±1.45	4.89±1.93	1.71	6.97
12	0.200	0.211	1.50±0.23	3.63±1.57	2.06±0.55	4.59±1.79	3.08±1.85	1.78	8.41
14	0.200	0.136	1.24±0.17	4.33±1.55	1.52±0.39	3.85±1.24	3.47±1.43	1.67	7.46
16	0.200	0.187	1.46±0.14	2.45±0.77	2.03±0.38	6.40±1.87	4.34±2.85	1.85	7.88
17	0.200	0.261	1.62±0.20	2.33±0.94	2.28±0.51	7.08±2.55	2.24±2.05	1.87	8.66
18	0.200	0.113	1.37±0.12	3.88±0.91	1.94±0.26	4.10±0.92	5.68±1.59	1.73	7.88
19	0.200	0.185	1.24±0.24	4.50±2.19	1.86±0.57	3.27±1.53	5.32±2.61	1.73	7.15
20	0.200	0.185	1.48±0.16	2.94±1.04	1.98±0.42	5.46±1.77	2.03±1.15	1.85	7.99
21	0.250	0.269	1.38±0.31	4.04±2.46	1.38±0.54	5.25±2.86	2.89±2.25	1.52	9.08
Mean[2]			1.40±0.18	3.40±1.38	1.96±0.44	5.11±1.71	3.97±2.12	1.79	7.79
SD[3]			0.20	1.06	0.33	1.74	2.04	0.10	0.69
Coeff. of var.			14%	31%	17%	34%	51%	6%	9%

[1] $\hat{\sigma} = S(\hat{\mathbf{\Theta}})/(r\text{-}5)$.
[2] For 10 replicates with $\sigma = 0.200$.
[3] Overall standard deviation of parameter estimates for 10 replicates with $\sigma = 0.200$.

TABLE 3.—Estimated parameters for 20 stochastic replicates of the deterministic model. The Levenberg-Marquardt algorithm is employed here in a three-dimensional parameter space (m, q, n). For each parameter and replicate, the parameter estimate ± its estimated standard deviation from Equation (12) are tabulated.

Replicate	σ	$\hat{\sigma}$[1]	$\hat{m}$ (10^6)	$\hat{q}$ (10^{-6})	$\hat{n}$	$\hat{f}_{MSY}$ (10^5)	$\hat{U}_{MSY}$
2	0.025	0.017	1.35±0.02	4.62±0.15	1.86±0.03	1.75	7.68
3	0.050	0.045	1.38±0.04	4.86±0.40	1.92±0.08	1.78	7.77
4	0.075	0.081	1.46±0.07	5.31±0.74	1.89±0.12	1.73	8.45
5	0.100	0.106	1.40±0.08	5.17±0.86	2.24±0.18	1.87	7.47
6	0.125	0.094	1.35±0.09	4.86±0.85	1.69±0.15	1.66	8.15
7	0.150	0.152	1.48±0.18	4.58±1.34	1.67±0.26	1.63	9.06
8	0.175	0.169	1.25±0.16	4.36±1.26	1.33±0.23	1.49	8.42
9	0.200	0.212	1.19±0.32	3.61±1.96	1.20±0.49	1.51	7.87
10	0.200	0.228	1.72±0.17	7.18±1.92	1.98±0.25	1.75	9.78
11	0.200	0.188	1.17±0.18	5.14±2.01	1.27±0.28	1.48	7.88
12	0.200	0.203	1.44±0.22	4.17±1.48	1.74±0.34	1.66	8.68
13	0.200	0.216	1.39±0.18	3.47±1.06	1.70±0.31	1.66	8.38
14	0.200	0.140	1.06±0.23	2.94±1.18	1.05±0.41	1.53	6.97
15	0.200	0.287	1.19±0.19	4.10±1.50	1.37±0.29	1.48	8.08
16	0.200	0.198	1.42±0.17	5.99±2.07	1.56±0.26	1.64	8.64
17	0.200	0.251	1.60±0.21	6.54±2.38	1.99±0.32	1.74	9.17
18	0.200	0.140	1.31±0.19	3.87±1.22	1.49±0.27	1.53	8.58
19	0.200	0.194	1.24±0.25	3.67±1.72	1.51±0.41	1.60	7.74
20	0.200	0.176	1.46±0.15	5.27±1.63	1.88±0.29	1.82	8.05
21	0.250	0.254	1.38±0.28	5.24±2.65	1.39±0.39	1.53	9.04
Mean[2]			1.35±0.21	4.66±1.72	1.56±0.33	1.62	8.32
SD[3]			0.19	1.34	0.31	0.11	0.73
Coeff. of var.			14%	29%	20%	7%	9%

[1] $\hat{\sigma} = S(\hat{\mathbf{\Theta}})/(r\text{-}3)$.
[2] For 12 replicates with $\sigma = 0.200$.
[3] Overall standard deviation of parameter estimates for 12 replicates with $\sigma = 0.200$.

CASE STUDIES

We applied the three-parameter method to the catch-effort data of the yellowfin tuna fishery of the eastern tropical Pacific, 1934 through 1967 [the same data that were analyzed by Pella and Tomlinson (1969) and by Fox (1971)]. Table 4 gives a comparison of results, and our final equilibrium model is shown by Figure 3. As indicated by Table 4, the parameter estimates of the Levenberg-Marquardt method are comparable with the estimates that Fox obtained with his search algorithm. Pella and Tomlinson also employed a searching algorithm but their minimization criterion was an unweighted least-squares function. Our standard deviation estimate is very small for $\hat{m}$(MSY) but relatively large for $\hat{B}_{\infty}$, $\hat{n}$, $\hat{q}$, and $\hat{B}_0$, which is a consequence of insufficient information in the yellowfin tuna data on yield at high fishing rates. With such limited information, one can anticipate that neither the shape nor the location of the descending portion of the equilibrium curve (dashed in Figure 3) could be determined with much accuracy, and the large variance estimates on the system coefficients reflect this situation. Of course, the variance estimates for $\hat{f}_{MSY}$ and $\hat{U}_{MSY}$ can always be calculated by the delta method, and to avoid the complex derivations that accompany the presence of covariance terms, an alternative would be to define a new parameter space so as to estimate f_{MSY} or U_{MSY} directly. The variance-covariance matrix for the coefficients would then provide the desired information on the variability of those parameters.

Our final example is based on the data from the Pacific halibut fishery in International Pacific Halibut Commission Area 2, as given in Ricker (1975, table 13.1). To analyze these data, Ricker derived an estimate of q from the age composition of the catch. Then he obtained parameter estimates for a Graham-Schaefer model by regressing $Y_E/\bar{B}$ against $\bar{B}$ and Y_E/f against f (Ricker 1975, examples 13.5 and 13.6). In both cases, Ricker employed GM and Nair-Bartlett regression. The results Ricker obtained by fitting the Graham-Schaefer model were compared with the results we obtained from fitting the generalized stock production model by our three-parameter version of the Levenberg-Marquardt method (Table 5). The latter provided estimates of m, q, and n with relatively small variance estimates. Furthermore, the estimate of n appears to be significantly different from 2.00, which validates the use of the Pella-Tomlinson model. Nevertheless, estimates of m are not significantly affected by the choice of the wrong model, while estimates of f_{MSY} are slightly

TABLE 4.—Comparison of parameter estimates obtained by Pella and Tomlinson (1969), by Fox (1971) and by the Levenberg-Marquardt algorithm for the yellowfin tuna in eastern Pacific Ocean. Values that follow the ± signs are the standard-deviation estimates for each parameter.

Reference	p	$\bar{B}_{\infty}$ (10^6)	n	q (10^{-5})	B_0 (10^6)	m (10^6)	f_{MSY}	U_{MSY}	Residuals
Pella and Tomlinson (1969, table 5)	—	—	1.40	45.0	—	1.826	35,300	5,173	1.78×10^{16}
Fox (1971, table 4)	—	1.427	2.10	8.10	1.206	1.926	32,700	5,890	0.736
Levenberg-Marquardt algorithm	—	1.448 ±0.890	2.08 ±0.75	8.01 ±4.9	1.192 ±1.24	1.924 ±0.90	32,700	5,884	0.735
Levenberg-Marquardt algorithm (correlated error)	0.27 ±0.25	1.274 ±0.653	2.30 ±0.55	9.08 ±4.7	1.079 ±0.553	1.962 ±0.106	32,170	6,097	0.641

TABLE 5.—Comparison between the estimates of Ricker (1975) for the Pacific halibut (International Pacific Halibut Commission Area 2) and those obtained by the Levenberg-Marquardt algorithm. Values that follow the ± signs are the standard-deviation estimates for each parameter.

Reference	p	B_{∞} (10^6)	n	q (10^{-7})	m (10^5)	f_{MSY}	U_{MSY}
Ricker (1975, example 13.5)							
GM regression	—	204	2.00	9.07	31.2	3.37	92.6
Nair-Bartlett regression	—	195	2.00	9.07	31.0	3.50	88.6
Ricker (1975, example 13.6)							
GM regression	—	256	2.00	9.07	33.0	2.84	116.2
Nair-Bartlett regression	—	239	2.00	9.07	31.8	2.94	108.2
Levenberg-Marquardt algorithm	—	187 ±18	1.28 ±0.09	14.45 ±1.36	31.6 ±0.83	2.83	111.7
Levenberg-Marquardt algorithm (correlated error)	0.33 ±0.16	188 ±22	1.28 ±0.12	14.33 ±1.67	31.8 ±1.0	2.84	112.0

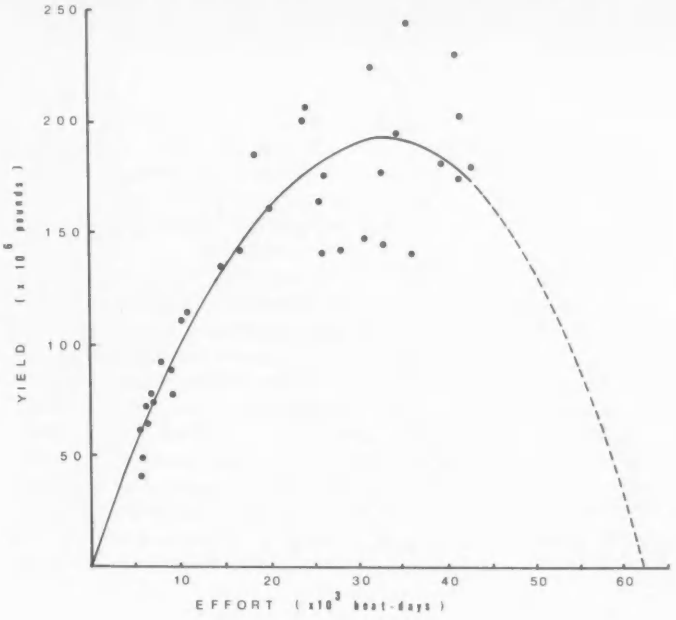

FIGURE 3.—Equilibrium stock production model for yellowfin tuna data, from 1934 through 1967, as determined by the Levenberg-Marquardt algorithm.

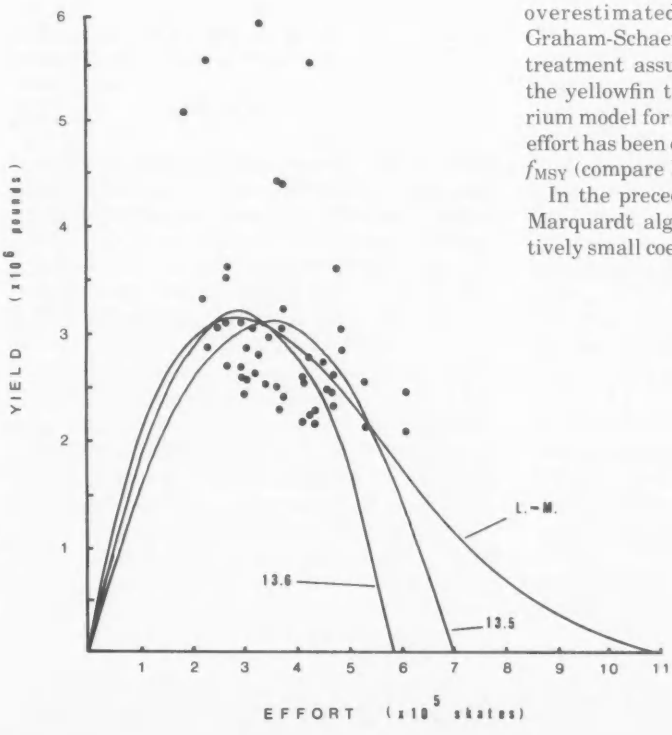

FIGURE 4.—Equilibrium stock production models for Pacific halibut (International Pacific Halibit Commission Area 2), from 1910 through 1957, as determined by Ricker (1975, examples 13.5 and 13.6, Nair-Bartlett regressions) and by the Levenberg-Marquardt algorithm (three-parameter version).

overestimated in most applications of the Graham-Schaefer model (note also that Ricker's treatment assumes equilibrium). In contrast to the yellowfin tuna data, analysis of the equilibrium model for halibut data indicates that fishing effort has been concentrated slightly to the right of f_{MSY} (compare Figures 3 and 4).

In the preceding case studies, the Levenberg-Marquardt algorithm gave estimates with relatively small coefficients of variation. In both cases,

e.g., the coefficients of variation for the estimates of maximum sustainable yield ($\hat{m}$) were below 6%. It is questionable, however, whether the data can justify such precision. Variability of the exploited population due to migration, to changes in fishery regulations over time, and to expansion of the fishing areas, as well as variability of q due to learning by fishermen and to technological developments, are important factors underlying the complexity of events influencing the serial catch-effort information. In future research, alternative forms of the model in which q is a variable parameterized with respect to time will be explored. Furthermore, in a randomly fluctuating environment, equilibrium population levels (and MSY, by extension) are not constant and the equilibrium points are instead described by a probabilistic cloud representing the equilibrium probability distribution (May 1974). The knowledge of this equilibrium probability distribution would give us some idea of the probability of achieving the desired management goal (MSY, for instance).

DISCUSSION ON ERROR STRUCTURE

In the preceding examples, we found runs in the time sequence plot of residuals. Those runs indicate correlations among the residuals. Serial correlation, as we usually find in applying production models to catch data, indicates that the real system is working differently than the presupposed model and that some minor effects have been neglected (such as age composition or environmental factors). But as indicated by Draper and Smith (1966), the effects of correlation can be ignored when the ratio $(r-p)/r$ tends to unity (p being the number of estimated parameters). In certain situations, of course, this ratio is likely to become small (tending to zero as r approaches p) and we may want to consider weights (W_i) which account for both the inequality of variance and the correlations. In our estimation procedure, the assumption of uncorrelated error can be relaxed by writing Equation (9) in the more general form (J. J. Pella, pers. commun.)

$$S(\hat{\Theta},\hat{\rho}) = [\mathbf{Y}-\hat{\mathbf{Y}}]\,\mathbf{W}^{-1}\,[\mathbf{Y}-\hat{\mathbf{Y}}]^{\mathrm{T}}, \qquad (22)$$

where $\mathbf{Y}$ is the row vector of observed yields, $\hat{\mathbf{Y}}$ is the row vector of predicted yields, and $\mathbf{W}$ is the symmetric, positive definite matrix

$$\mathbf{W} = \begin{bmatrix} \hat{Y}_1^2 & \hat{Y}_1\hat{Y}_2\hat{\rho} & \cdots & \hat{Y}_1\hat{Y}_r\hat{\rho}^{(r-1)} \\ \hat{Y}_1\hat{Y}_2\hat{\rho} & \hat{Y}_2^2 & \cdots & \hat{Y}_2\hat{Y}_r\hat{\rho}^{(r-2)} \\ \vdots & \vdots & \ddots & \vdots \\ \hat{Y}_1\hat{Y}_r\hat{\rho}^{(r-1)} & \hat{Y}_2\hat{Y}_r\hat{\rho}^{(r-2)} & \cdots & \hat{Y}_r^2 \end{bmatrix}.$$

Parameter ρ, constrained between 0 and 1, is a measure of the importance of lags and can be estimated along with the parameters of the differential equations (1) and (3). It can be seen that Equation (9) is a particular case of Equation (22), where the off-diagonal elements of $\mathbf{W}$ are null.

The Levenberg-Marquardt algorithm, as formulated in Equation (11), is designed to minimize directly a sum of squares of residuals as given by Equation (9). In order to minimize Equation (22) by using Equation (11), we must scale $\mathbf{W}$ by the transformation

$$\mathbf{X} = \mathbf{D}^{-1}\,\mathbf{W}\,\mathbf{D}^{-1}, \qquad (23)$$

where $\mathbf{D}$ is a diagonal matrix having elements $D_{ii} = \hat{Y}_i$ $(i = 1, \ldots, r)$, and write $\mathbf{W}$ as

$$\mathbf{W} = \mathbf{D}\,\mathbf{U}\,\Lambda\,\mathbf{U}^{\mathrm{T}}\,\mathbf{D}, \qquad (24)$$

where $\mathbf{U}\Lambda\mathbf{U}^{\mathrm{T}}$ is the eigenvalue and eigenvector decomposition of $\mathbf{X}$. Note that $\mathbf{X}$ is actually the correlation matrix of errors. Therefore Equation (22) becomes

$$S(\hat{\Theta},\hat{\rho}) = [\mathbf{Y}-\hat{\mathbf{Y}}]\,\mathbf{D}^{-1}\,\mathbf{U}\,\Lambda^{-1}\,\mathbf{U}^{\mathrm{T}}\,\mathbf{D}^{-1}\,[\mathbf{Y}-\hat{\mathbf{Y}}]^{\mathrm{T}}. \qquad (25)$$

Then Equation (25) has the same form as Equation (9), where the weights (W_i) are the square roots of the eigenvalues of $\mathbf{X}$ and where the residuals are given by $[\mathbf{Y}-\hat{\mathbf{Y}}]\,\mathbf{D}^{-1}\,\mathbf{U}$. Such a procedure requires, however, diagnoalization of an r by r matrix. Moreover, diagonalization must be repeated at least p times for each iteration. This procedure produces a 10-fold increase in computing time.

Although an exhaustive study of all possible stochastic effects on the model was not attempted, some simulations were done to determine the magnitude of error in parameter estimates due to serial correlations of the ϵ_i. Results are given on Tables 4 and 5. For the yellowfin tuna data, $\hat{\rho}$ =

0.27. For the Pacific halibut data, $\hat{\rho} = 0.33$. In either case, $\hat{\rho}$ exhibits a relatively large coefficient of variation when compared with the elements of $\hat{\boldsymbol{\Theta}}$. One could anticipate such results since ρ reflects the "persistence" of fluctuations in population size, and the estimation of ρ would therefore require a longer catch history in order to achieve a greater precision. But more importantly, the values of $\hat{\boldsymbol{\Theta}}$ and $\mathrm{Var}[\hat{\boldsymbol{\Theta}}]$ were not significantly altered by the inclusion of the additional parameter. And while the errors of any particular catch history might indeed by correlated, the minimization criterion (9) will provide satisfactory estimates of $\boldsymbol{\Theta}$ despite the fact that correlations do not enter into its formulation. The limited results contained herein suggest that serial correlation can be safely ignored when the ratio $(r - p)/r$ is near unity. Under such a condition the estimation procedure is robust with respect to the assumption of independence of errors in actual data.

CONCLUSION

The purpose of this paper has been to examine a version of the Levenberg-Marquardt algorithm as an alternative method for estimating the coefficients of the generalized stock production model. The parameter values obtained by this procedure are close to those obtained by previous studies on yellowfin tuna and Pacific halibut. Obviously, data requirements are such that a full range of effort values (ranging over low and high exploitation rates) are necessary to insure convergence in the estimation procedure and to produce estimates with small variability. Our simulations reveal that with the Levenberg-Marquardt method both the estimates of coefficients and the estimates of variances remain approximately unbiased when white noise is considered. If present, such bias is sufficiently small as to be obscured in the variability associated with catch error. The simulations also showed the range of variability in parameter estimates that might be expected for given levels of normally distributed error in catch data.

Because the parameters of interest appear explicitly in the system equations, the estimation procedure for the parameters also produces the variance estimates directly. Moreover, the method has a reliability and an efficiency of computation somewhat greater than previous methods. And since the estimation procedure relies on a numerically integrated system of differential equations, modifications of the model to incorporate such hypothetical effects as migration or stock interactions can be made easily. Of course, to the extent that the estimation procedure must rely strictly on catch-effort data, it will be subject to the same information uncertainties as any other method. But within the basic estimation procedure, we can combine the catch-effort data with prior information and thereby reduce the uncertainties in our estimates. The prior information can be any information on a state variable, such as $B(t)$, or even any prior knowledge of the coefficients as expressed by $\hat{\boldsymbol{\Theta}} \pm \mathrm{Var}(\hat{\boldsymbol{\Theta}})$. Suppose, for example, that we have information from independent surveys on stock density (acoustic surveys, indirect estimation from knowledge of larval densities, or even virtual population analysis from catch records). Such surveys would then provide us with estimates $\hat{B}_t$ each having a variance $V(\hat{B}_t)$, let us say, at various times t. We can easily introduce such information into the estimation procedure by defining the new objective function

$$S(\hat{\boldsymbol{\Theta}}) = \sum_i W_i(Y_i - \hat{Y}_i)^2 + \sum_j V_{B_j}^{-1}(B_j - \hat{B}_j)^2. \quad (26)$$

Introduction of the second term in the objective function constrains the optimization and thereby improves convergence. If the prior information has extremely large variance, then this information is of no value; the second term of Equation (26) will tend to zero and the objective function then reduces to Equation (9). In general, the alteration permits the simultaneous employment of the two state variables. Therefore, the final coefficients are no longer based solely on catch and effort data; their determination includes our knowledge of previous stock densities.

As observed here in a statistical setting, and by Fletcher (1978a, b) in the exact analysis, the Pella-Tomlinson system exhibits internal instability in its parametric relationships. That behavior arises from the variable nature of the system's nonlinearity, which would not be particularly detrimental if our problems were limited strictly to the geometric syntheses of data by curve fitting. But for the purposes of management and preservation of stocks, the subject is elevated partly at least to the status of parameter estimation "where we look for procedures to obtain values of the parameters that not only fit the data well, but also come on the average fairly close to the true value" (Bard 1974). Although the Pella-

Tomlinson system exhibits a convenient flexibility with a minimum number of coefficients, the peculiar coupling of the coefficients to the nonlinearity of the system often provides more flexibility than we care to have, and a conventional least-squares statistic may not be sufficient to control the system in the estimation procedure. In consequence, many constraints have to be imposed on the system in order to obtain convergence in the estimation procedure and to insure reliability in the coefficient values thus estimated.

ACKNOWLEDGMENTS

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SYSTEMATICS AND ZOOGEOGRAPHY OF THE PORCUPINEFISHES (*DIODON*, DIODONTIDAE, TETRAODONTIFORMES), WITH COMMENTS ON EGG AND LARVAL DEVELOPMENT[1]

JEFFREY M. LEIS[2]

ABSTRACT

The porcupinefish genus *Diodon* is composed of five species: *D. hystrix* Linnaeus and *D. eydouxii* Brissout de Barneville are closely related species, each of which has a relatively elongate body, spines on the caudal peduncle, and high dorsal and anal fin ray counts; *D. holocanthus* Linnaeus and *D. liturosus* Shaw form a second species pair, each of which has a round body, no caudal peduncle spines, and moderate dorsal and anal fin ray counts; *D. nicthemerus* Cuvier is a round-bodied species but differs from *D. holocanthus* and *D. liturosus* in meristic characters and spination.

Diodon hystrix, *D. holocanthus*, and *D. eydouxii* are distributed circumtropically. The Atlantic population of *D. holocanthus* has diverged from the Indo-Pacific (including eastern Pacific) populations. *Diodon eydouxii* is pelagic, and both *D. hystrix* and *D. holocanthus* have pelagic juvenile stages. *Diodon liturosus* is found in the Indo-West Pacific, and *D. nicthemerus* is limited to Tasmania and southern Australia. It is not known whether the latter species have pelagic stages.

The egg and larval stages of *D. hystrix* and *D. holocanthus* (the latter identified by rearing) are similar. The pelagic eggs are 1.6-2.1 mm in diameter and hatch in about 5 days at 25°C. The larvae metamorphose to spiny juveniles at ca. 4 mm in about 3 wk. Both species have pelagic juvenile stages of long duration: *D. hystrix* remains pelagic to ca. 200 mm standard length, thus providing ample time for dispersal. Eggs and larvae of the other species are unknown.

The identities of the species of the genus *Diodon* have been confused since the time of Linnaeus. The most recent description of a valid "new" species was in 1846, but, unfortunately, time has done little to clarify the situation. Twenty-eight nominal species attributable to *Diodon* have been described since 1758, and most contemporary authors recognize two or three species. However, Le Danois (1959), in the only recent review of the genus as a whole, recognized six species.

The present study grew out of attempts to identify juvenile *Diodon* that resulted from rearing of pelagic eggs taken in Kaneohe Bay, Oahu, Hawaii (Watson and Leis 1974). These juveniles could not be identified using existing keys. While current literature recognized only two species of *Diodon* in Hawaiian waters, examination of museum specimens revealed that three were present there. This discovery, together with the encouragement of J. E. Randall of the Bernice P. Bishop Museum, led to the present study clarifying the identities of all of the species of *Diodon* and the description of their development. An attempt was made to obtain information on existing type-specimens and this, along with the examination of a large number of specimens, has led to the conclusion that the genus is composed of five species, three of which are distributed circumtropically. Further, it is shown that the present taxonomic confusion is attributable to inadequate original descriptions, reliance on poor characters for differentiation, the close similarity of several of the species, and unusual aspects of the life histories of the species of *Diodon*. All of the nominal species could be distinguished with some certainty with two exceptions: the type of *Diodon echinus* Rafinesque 1810 could not be located and the original description provides no clue to its identification; the holotype of *Trichocyclus erinaceus* Günther 1870 (BMHN 1976.2.23.1) is a small fish in especially poor condition, giving the appearance of having been obtained from a stomach of some predator, and, while it is certainly a *Diodon*, more specific identification could not be made. *Diodon dussumieri* Bibron (see Le Danois 1959, 1961) is a nomen nudum, but examination of the "type" (MNHN 1306) by J. E. Randall of the Bernice P. Bishop Museum indicates that Le Danois was correct in placing *D. dussumieri* in synonomy with *D. holocanthus*.

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Although basically shorefishes, the diodontids (at least *Diodon* and *Chilomycterus*) are strongly tied to the pelagic environment through pelagic eggs and well-developed pelagic juvenile stages. In *Diodon* these juveniles remain pelagic for weeks or months (judging from size) and are often found far from shore. In fact, juvenile *Diodon* spp. are commonly encountered in the stomachs of such pelagic predators as dolphins (Gibbs and Collette 1959), and one species, *D. eydouxii*, is apparently pelagic throughout its life cycle.

The eggs of diodontids are poorly known. Nichols and Breder (1926) described the unfertilized eggs of *Chilomycterus schoepfi* from New Jersey as demersal, nonadhesive, transparent, and about 1.8 mm in diameter. However, Breder and Clark (1947) suggested that the eggs of *C. schoepfi* may be normally pelagic. The pelagic eggs of *D. holocanthus* and *D. hystrix* from Hawaii were briefly described as *Diodon* sp. and "diodontid II," respectively, by Watson and Leis (1974). Sanzo (1930) described the development of what are apparently the pelagic eggs of *D. hystrix* (identified as *Crayracion* sp.?) from the Red Sea. Wolfsheimer (1957) reported an aquarium spawning of *D. holocanthus* (identified by him as *D. hystrix*), but provided little descriptive information on the eggs. The eggs mentioned by Wolfscheimer sank, but did not adhere, to the bottom of the aquarium. They did not develop, so it is likely that they were not fertilized.

Larval and juvenile *Diodon* are no better known than the eggs. Blanco and Villadolid (1951) illustrated a juvenile "*Diodon bleekeri*," but this fish is clearly a juvenile tetraodontid. Many juvenile tetraodontids have prominent spines, particularly on the ventral surfaces. Fowler (1928) illustrated a juvenile *Diodon*, identified as *D. hystrix*, but the figure does not show spines on the caudal peduncle (see below), so this identification is apparently incorrect (assuming the drawing is accurate). No locality or other descriptive data are given by Fowler, so a specific identification cannot be made. Sanzo (1930) illustrated two larvae that resulted from rearing of his *D. hystrix* eggs and a juvenile *Diodon* captured in a plankton tow. The illustration of this latter fish shows no peduncle spines, but in other respects it resembles *D. hystrix*. Mito (1966) illustrated a larval and a juvenile *Diodon*, both identified as *D. holocanthus*. The pigmentation and the relatively small eye shown in Mito's illustrations more closely resemble the specimens of *D. hystrix* studied here. At least four species of *Diodon* occur in Japanese waters, and Mito's specimens could be any of these, because he gives no information as to how the identifications were made. Nishimura (1960) reported on juvenile *Diodon* cast ashore in the Sea of Japan, but did not provide specific identifications.

MATERIALS AND METHODS

Measurements and counts are as defined by Hubbs and Lagler (1958:19-28) unless otherwise stated. Measurements routinely were made with needle point dividers to the nearest 0.5 mm. Fish <10 mm and all eggs were measured under a dissecting microscope to the nearest division of the ocular micrometer (±0.02 mm at 50×, the power normally used). All measurements are from preserved specimens.

Unspecified lengths are in millimeters standard length. Caudal peduncle length was measured from the posterior base of the dorsal fin to the end of the hypural plate. Head width was measured immediately behind the eyes. Body width was measured at the base of the pectoral fin. Width of the eye was taken horizontally across the clear cornea. Measurements are given as proportions of standard length.

Dorsal and anal fin ray counts included all rays, branched and unbranched. The last two rays were counted separately because they have separate bases. Pectoral fin ray counts excluded the upper ray. This ray, although well developed in small (<30 mm) juveniles, is a rudiment in adults and is often not visible because it is embedded. In large specimens, the fin bases are especially fleshy and accurate fin ray counts are difficult to make without dissection or radiography.

Body measurements are given as range, mean ($\bar{x}$), and standard deviation (SD). The sample size for the measurements is given in parentheses at the beginning of the description of each species. Morphometrics are included only from individuals >50 mm. Fin ray counts are included for all specimens on which counts could be made (Table 1). In most cases, rays in both pectoral fins were counted. Fin rays were not counted on specimens with fin damage or on specimens that had rays obscured due to the thick bases of the dorsal and anal fins. Radiography was tried unsuccessfully to obtain vertebral counts: the dermal spines and their bases obscured the vertebrae, and made accurate counts impossible. The vertebral counts

TABLE 1.—Fin ray counts of *Diodon* species.

Dorsal fin rays	12	13	14	15	16	17	18	$\bar{x}$
D. eydouxii								
Atlantic						3	1	17.25
Indo-Pacific					4	25	6	17.06
D. hystrix								
Atlantic				2	7	1		15.90
Indo-Pacific			2	20	8			15.20
D. holocanthus								
Atlantic			22	4				14.15
Indo-Pacific		9	39	7				13.96
D. liturosus			1	12	15			15.50
D. nicthemerus	1	10						12.91

Anal fin rays	12	13	14	15	16	17	18	$\bar{x}$
D. eydouxii								
Atlantic						3	1	17.25
Indo-Pacific					2	22	11	17.26
D. hystrix								
Atlantic				3	7			15.70
Indo-Pacific			1	15	6			15.23
D. holocanthus								
Atlantic		9	18					13.67
Indo-Pacific		26	27	1				13.54
D. liturosus			10	17	1			14.68
D. nicthemerus	3	5	2					12.80

Pectoral fin rays	19	20	21	22	23	24	25	$\bar{x}$
D. eydouxii								
Atlantic			5	3				21.38
Indo-Pacific	7	58	17					20.12
D. hystrix								
Atlantic				1	10	10	1	23.50
Indo-Pacific			2	16	34	6		22.76
D. holocanthus								
Atlantic			7	31	20			22.22
Indo-Pacific		1	17	57	27	5		22.17
D. liturosus			2	11	24	17	2	23.11
D. nicthemerus	2	9	9					20.35

given for *D. holocanthus* were made on cleared and stained material.

The dermal spines require special terminology and measurements, as given below. Measurements, except for shaft length, were taken on dissected spines (Figure 1).

The spine shaft is that portion bearing the pointed tip, but excluding the shaft extension. The length of the spine (= shaft length) was taken from the lower portion of the lateral arm to the tip of the shaft. The starting point for this measurement can be found most easily by probing around the base of the spine.

The shaft extension is the portion of the shaft extending past the lateral arms of the base, and its length was measured from the lower portion of the lateral arm to the tip of the extension.

The lateral arms of the base are the subdermal portions of the spine upon which the spine pivots during erection. The length of the spine base was the straight line distance from tip to tip of the lateral arms.

The frontal spines are those of the anteriormost row on the head between the eyes. The pectoral axil spines are the spines immediately posterior to the base of the pectoral fin.

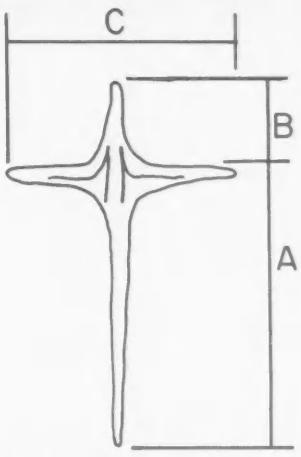

FIGURE 1.—Typical *Diodon* body spine: (A) spine (or shaft) length, (B) length of the shaft extension, (C) length of the spine base. The tip of the spine shaft points caudad.

The number of spines in a longitudinal row over the dorsum from the snout to the dorsal fin base (S-D spines) and the spines in a longitudinal row over the ventrum from the lower jaw to the anus (S-A spines) were counted. These rows of spines are irregular and difficult to follow, so the counts should be considered approximate. With practice, repeated counts of ±1 can be achieved consistently. The numbers of spines between pectoral fins, both over the dorsum (P-D-P spines) and ventrum (P-V-P spines), were also counted, but these counts are even less reproducible than the longitudinal counts.

Repeated reference is made to the spines on the caudal peduncle. In some species the only spines in the region of the caudal peduncle are some rather large spines associated with the dorsal and anal fin bases. Although these spines extend over the peduncle, their subdermal bases (lateral arms and shaft extension) are at least partially anterior to a line between the base of the posteriormost rays of the dorsal and anal fins, and they are considered not to be on the peduncle. In other species, there are relatively small spines which are wholly posterior to the line defined above on the dorsal and dorsolateral surfaces of the peduncle; these spines are considered to be on the peduncle (Figure 2).

Larvae were obtained from plankton samples (field specimens) and rearing experiments using eggs from plankton tows (reared specimens). All eggs and larvae were captured around the Hawaiian island of Oahu. Rearing took place in

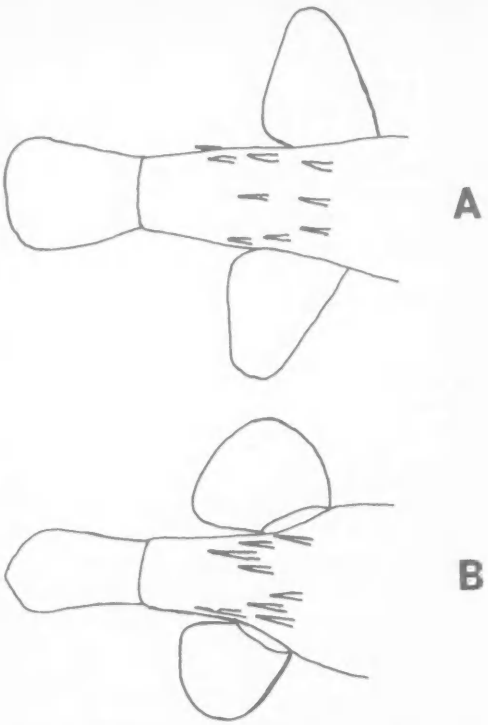

FIGURE 2.—Semidiagrammatic lateral view of the caudal peduncle and posteriormost spines of (A) a slender-bodied, long peduncled species (*Diodon eydouxii*) and (B) a round-bodied, short peduncled species (*D. holocanthus*).

the laboratory under ambient temperature (ca. 25°C) and a variety of conditions. Generally, the eggs were hatched in unaerated 4-l beakers filled with seawater from the collection area. Hatched larvae were transferred to 10-20 l containers and provided with overhead illumination. The containers were wrapped in black plastic. Wild zooplankton (ca. 60-200 μm) from a plankton pump were added on alternate days; this was later supplemented with *Artemia* nauplii. Water was changed twice a week and specimens were removed periodically for preservation. Many rearing attempts were made, but since fewer than 20 eggs usually were available per attempt, few of the attempts were successful.

Some larvae were cleared and stained using the KOH-alizarin red method of Hollister (1934). Measurements and definitions of stages generally follow those of Leis (1977), unless otherwise noted. All drawings of eggs and larvae were made with the aid of a camera lucida.

The institutions housing the examined specimens are as follows: Academy of Natural Sciences of Philadelphia (ANSP); Australian Museum, Sydney (AMS); Bernice P. Bishop Museum, Honolulu (BPBM); British Museum (Natural History) (BMNH); California Academy of Sciences (CAS); Gulf Coast Research Laboratory and Museum (GCRL); George Vanderbilt Foundation (GVF), deposited in CAS; Hawaii Institute of Marine Biology (HIMB); Los Angeles County Museum of Natural History (LACM); Museum National d'Histoire Naturelle, Paris (MNHN); National Marine Fisheries Service, Honolulu, Hawaii (NMFS H), La Jolla, Calif. (NMFS LJ), and Miami, Fla. (NMFS M); Naturhistorisches Museum, Vienna (NMV); J. L. B. Smith Institute of Ichthyology at Rhodes University, South Africa (RUSI); Scripps Institution of Oceanography (SIO); Tulane University (TU); National Museum of Natural History, Smithsonian Institution (USNM); University of Arizona (UA). A catalog number is given when available; many GVF specimens were uncataloged and therefore the register or station number is given.

The synonymies include all known original usage of names. In addition, references of systematic or zoogeographic interest are included. If the identification of a nominal species is questionable, it is preceded by a question mark (?). Pre-Linnaean literature is cited in the text if appropriate, but is omitted from the synonymies.

GENUS *DIODON* LINNAEUS

Diodon Linnaeus 1758:334, after Artedi 1738. Type-species *D. hystrix* Linnaeus by subsequent designation of International Commission on Zoological Nomenclature, opinion 77.

Paradiodon Bleeker 1865:49. Type-species *D. hystrix* Linnaeus by original designation.

Trichodiodon Bleeker 1865:49. Type-species *D. pilosus* Mitchill by original designation.

Trichocyclus Günther 1870:316. Type-species *T. erinaceus* Günther by monotypy.

Diagnosis.—Body rotund, width 0.25-0.54, depth varies greatly depending on degree of inflation. Eyes large, 0.05-0.17. Swim bladder bilobed. Teeth in each jaw fused into a single beaklike unit without a median suture dividing upper or lower jaws into right and left halves. Gill opening a short, vertical slit immediately anterior to the

pectoral fin base. Approximately 20 vertebrae. Dorsal and anal fins usually rounded, set far back on body, with 12-18 rays. Caudal rounded, with 9 rays (there are no secondary rays). Pectoral fin slightly emarginate, with 19-25 rays, the uppermost ray (not counted) greatly reduced in adults. No pelvic fins. Body covered with long spines, all but a few (around the gill opening, dorsal fin base, and caudal peduncle) of which are erectile. Erectile spines consisting of a long pointed shaft, two subdermal lateral bases lying in nearly the same plane as the shaft, and usually a shaft extension which is shorter than the shaft. The shaft extension may be greatly reduced. Nasal organs consisting of a short tentacle with a pair of lateral openings near the tip. In larger individuals of some species the tissue closing the end of the tentacle may be absent, giving rise to a bifid nasal tentacle without nostrils. Both species whose reproductive habits are known (*D. hystrix* and *D. holocanthus*) spawn pelagic spherical eggs of 1.6-2.1 mm in diameter.

Remarks.—Only Bleeker's (1865) proposal of *Paradiodon* for the species here considered to belong in *Diodon* (because of page priority, he believed *Diodon* should apply to those species usually referred to *Chilomycterus*) has disturbed the stability of the usage of the name *Diodon*. *Trichodiodon* and *Trichocyclus* are names applied to juvenile stages of *Diodon*.

Although subgeneric status seems unwarranted, *Diodon* can be broken into two groups on the basis of body width, caudal peduncle length, and squamation. The species of the slender-bodied group, *D. eydouxii* and *D. hystrix*, have a rather narrow body (Figure 3, Table 2), long caudal peduncle (Figure 3, Table 2), and several small spines in the dorsal and dorsolateral surfaces of the peduncle. The species of the round-bodied group, *D. holocanthus*, *D. liturosus*, and *D. nicthemerus*, have a wider body, shorter caudal peduncle (Figure 3), and lack spines on the caudal peduncle (although there are strong spines, projecting over the peduncle, at the base of the dorsal and anal fins). Upon inflation, the dorsal and anal fins are engulfed by the expanding skin. In the round-bodied group, the caudal peduncle and fin are also largely obscured in inflated specimens and the large spines mentioned above provide added protection. In the slender-bodied group, the peduncle remains largely uncovered and is protected only by the relatively small spines on its upper surfaces. *Diodon nicthemerus*, although clearly a member of the round-bodied group, appears to have undergone a reduction in spine number and base size, and is thus separable from *D. holocanthus* and *D. liturosus*.

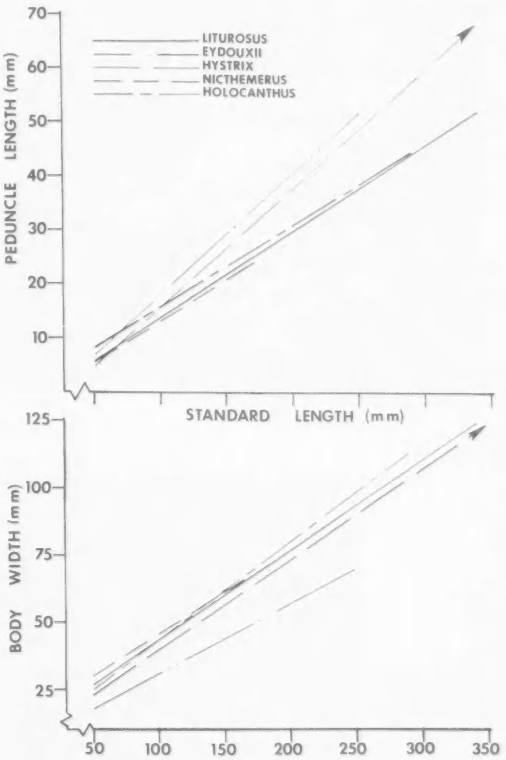

FIGURE 3.—Plotted regression lines of (top) caudal peduncle length vs. standard length and (bottom) body width vs. standard length for the five species of *Diodon*. Lines plotted only over size range of specimens examined. The line with arrow head for *D. hystrix* extends to 571 mm SL. Regression data in Table 2.

TABLE 2.—Regression equations for caudal peduncle length (PL) and body width (BW) vs. standard length (SL) in the five species of *Diodon* (see also Figure 3).

Species	Regression equation	r	t_{slope}	df
D. hystrix	PL = 0.189 SL − 2.79	0.97	21.16	31
D. eydouxii	PL = 0.226 SL − 4.79	0.95	17.44	33
D. liturosus	PL = 0.159 SL − 2.40	0.96	17.88	26
D. nicthemerus	PL = 0.151 SL − 1.38	0.94	7.85	8
D. holocanthus	PL = 0.152 SL + 4.69	0.90	15.86	61
D. hystrix	BW = 0.338 SL + 6.01	0.97	23.41	31
D. eydouxii	BW = 0.262 SL + 5.27	0.88	10.45	33
D. liturosus	BW = 0.333 SL + 10.29	0.90	10.58	26
D. nicthemerus	BW = 0.313 SL + 13.11	0.93	6.44	6
D. holocanthus	BW = 0.368 SL + 6.29	0.96	25.75	62

KEY TO THE SPECIES OF THE GENUS *DIODON*

1a Two or more small spines wholly on the dorsal or dorsolateral surfaces of the caudal peduncle (Figure 2A); color pattern of adults dominated by small (smaller than eye) spots; at least D, P, and C fins of adults with dark spots 2

1b No spines wholly on the caudal peduncle (Figure 2B); color pattern of adults dominated by large dorsal and lateral bars or blotches; fins of adults without spots except in some cases at base 3

2a P 19-22, both D and A 16-18; D and A of adults falcate; S-A spines ≤14; head width less than 30% SL ..... *D. eydouxii*
(circumtropical, oceanic)

2b P 22-25 (rarely 21), D 14-17, A 14-16; D and A of adults rounded; S-A spines ≥14; head width greater than 30% SL ..... *D. hystrix*
(circumtropical, shore fish but juveniles pelagic)

3a No small, fixed, tribase spine immediately above the gill opening; no small, flat spines on the anterior border of the depression surrounding the gill opening (Figure 4); S-A spines ≤11; adult color pattern dominated by four large lateral bars, dorsum uniformly dark ..... *D. nicthemerus*
(Australia)

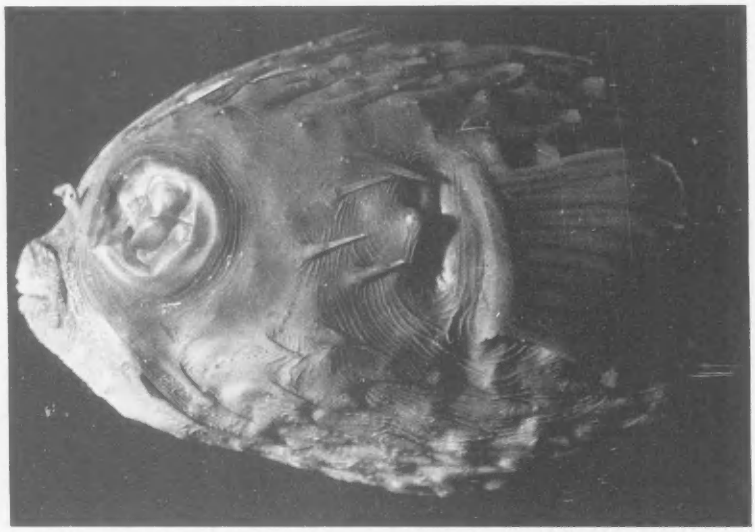

FIGURE 4.—Head of *Diodon nicthemerus* (AMS I.16990-004) showing arrangement of spines in the region of the gill opening. Note that spines anterior to gill opening are not flattened. Also note tubular nostril.

3b One or two small, fixed, tribase spines above the gill opening; three or four small, flat spines forming the anterior border of the depression surrounding the gill opening (Figure 5); S-A spines ≥12; adult color pattern dominated by several dorsal blotches 4

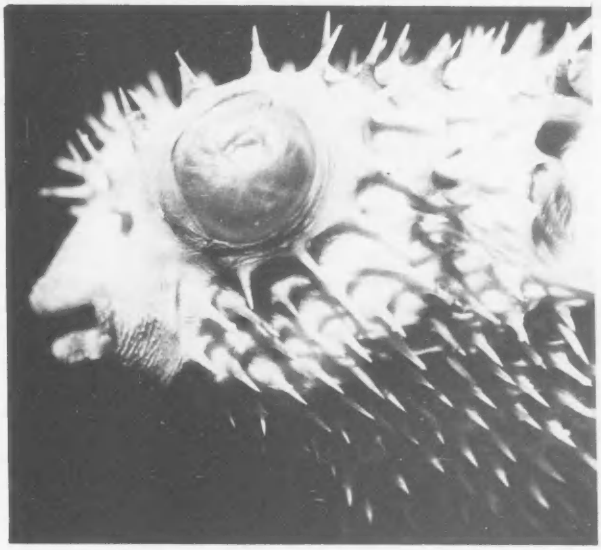

FIGURE 5.—Head of *Diodon liturosus* (CAS 30967) showing arrangement of spines in the region of the gill opening. Note that spines on anterior border of opening are short and flattened. Also note the small downward-pointing spine below the anterior border of the eye.

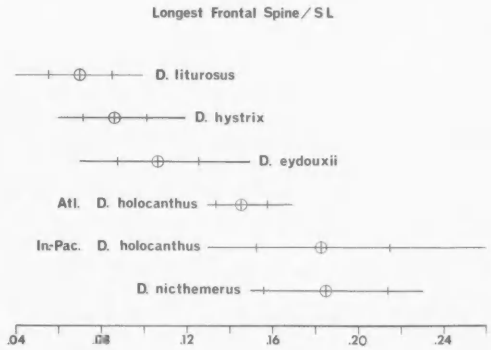

FIGURE 6.—Ratio of frontal spine length to standard length for the five species of *Diodon*. Line indicates range, circle and bar indicate mean, and vertical bars alone denote ±1 SD. Note difference of spine length between Atlantic and Indo-Pacific specimens of *D. holocanthus*. Number of specimens given in description for each species.

4a Frontal spines 0.04-0.10 (Figure 6), much shorter than pectoral axil spines; 17-22 S-A spines; a small downward-pointing spine below the anterior margin of the eye present; dorsal blotches with a distinct light border; a dark gular band from eye to eye under the lower jaw ..... *D. liturosus* (Indo-Pacific)

4b Frontal spines 0.13-0.28 (Figure 6), slightly shorter to much longer than pectoral axil spines; 12-15 S-A spines; a small downward-pointing spine below the anterior margin of the eye absent (Indo-Pacific specimens) or present (most Atlantic specimens); dorsal blotches without a distinct light border; no gular band ..... *D. holocanthus* (circumtropical)

DIODON EYDOUXII BRISSOUT DE BARNEVILLE

Pelagic Porcupinefish (Figure 7)

Diodon eydouxii Brissout de Barneville 1846:142 (eastern Pacific); Troschel 1847:364; Duméril 1855:278.

Diodon melanopsis Kaup 1855:228 (no locality given).

Diodon spinosissimus (not of Cuvier): Günther 1870:307 (Cape of Good Hope, Siam).

Diagnosis.—A slender-bodied *Diodon*, head width 0.25-0.30, peduncle length 0.16-0.22. Caudal peduncle armed dorsally with short spines. Body spines long and slender, moderate in number, S-D spines 13-17, S-A spines 10-14. Pectoral axil spines 0.11-0.16, usually longer than longest frontal spines. A short, fixed tribase spine immediately above gill opening. D 16-18, A 16-18, P 19-22. Nasal tentacle with a pair of lateral openings. No barbels or fleshy tentacles. Dorsal and anal fins falcate (rounded in juveniles). Color pattern dominated by small (ca. = to pupil) dark spots dorsally and laterally. These often associated with the spine axils. A dark gular band starting from below the eyes and continuing under the chin, usually with a branch extending dorsally between eye and gill opening.

Description.—(35 specimens) D 16-18, A 16-18, the first two or three rays unbranched; P 19-22. Head width 0.25-0.30 ($\bar{x}$ = 0.27; SD = 0.01), body width 0.25-0.35 ($\bar{x}$ = 0.30; SD = 0.02), peduncle length 0.16-0.22 ($\bar{x}$ = 0.19; SD = 0.02), eye 0.05-0.10 ($\bar{x}$ = 0.08; SD = 0.01). Dorsal and anal fins falcate, not rounded. Nasal tentacles with a pair of lateral openings.

S-D spines 13-17, S-A spines 10-14, about 12 spine rows over the dorsum between pectoral fin bases, about 21 spine rows over the ventrum between pectoral fin bases. Four or five frontal spines. Longest frontal spine 0.07-0.15 ($\bar{x}$ = 0.11; SD = 0.05), pectoral axil spines 0.11-0.16 ($\bar{x}$ = 0.14; SD = 0.01). Pectoral axil spines usually the longest on the body, 0.61-1.03 ($\bar{x}$ = 0.78; SD = 0.11) in frontal spines. Spines long and slender. Frontal, middorsal, and ventral spines of about the same length. Pectoral axil spines and those dorsolateral spines from over eye to over pectoral fin among the longest on body (ca. 0.8 in frontal spines). Spines on caudal peduncle short (ca. 1.5 in frontal spines) and fixed due to a rather long shaft extension (ca. 2 in shaft). Shaft extension on other spines reduced, never more than 15% of the shaft length. Subdermal bases moderate in extent, and, except for spines around fin bases and caudal peduncle, always shorter than shaft. No spines markedly reduced other than on caudal peduncle; the latter spines generally arranged in one or two bilateral pairs along the dorsolateral edge of the peduncle. Approximately 40% (14 of 36) of the specimens examined also possess a single dorsomedial spine on the caudal peduncle. A short, fixed tribase spine immediately above the gill opening and a second slightly posterior to it above the pectoral base. Three short, flat spines

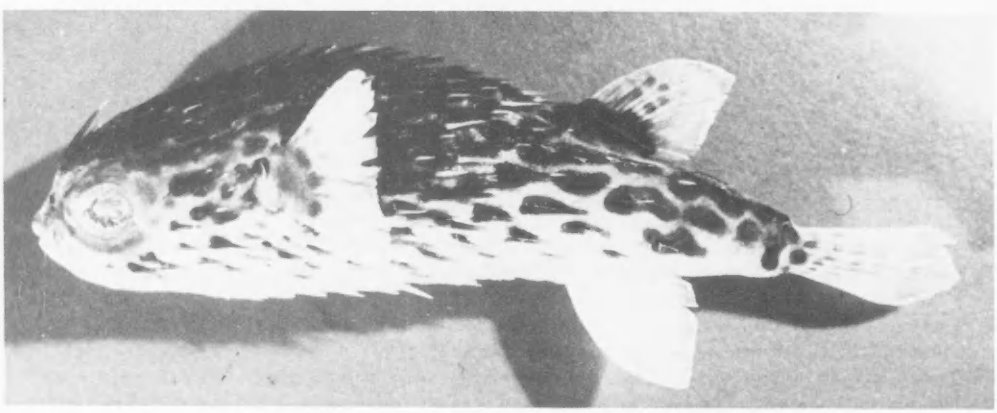

FIGURE 7.—*Diodon eydouxii*, 128 mm SL, central Pacific (NMFS H CHG 55-71).

with broad lateral bases form the anterior border of the gill opening. No spines on the snout.

No barbels or fleshy tentacles.

Dorsally the ground color is light grey to brown grading to white ventrally. Dorsal and lateral surfaces marked with dark ovoid spots (<eye diameter in length) most of which are associated with the spine axils, particularly on the sides posterior to the pectoral fin. Caudal peduncle usually mottled dorsally. Round spots (often diffuse) present on dorsal, pectoral, and caudal fins (caudal spots first seen on 100-mm fish, other fin spots begin to form between 30 and 100 mm). The pectoral spotting is limited to two vertical rows of four to six spots each. The anal fin is often dusky but never spotted. A dark gular band extends from the eye downward and forward, generally paralleling the ventral outline of the head. Usually a branch of this band extends dorsally between the eye and gill opening and is often discontinuous with the gular band. Specimens <100 mm usually have four opposed spots on the iris.

In life the dorsal ground color is medium to dark blue while the dorsal and lateral spots and gular band are dark blue to black. The ventral surfaces are silvery-white and the fins greyish (from a color transparency provided by R. Rosenblatt, SIO).

The largest specimen examined is 252 mm, but the next largest is only 177 mm, apparently a fairly small species. Twelve specimens (125-153 mm) were sexed although none were ripe: 7 males and 5 females.

Eggs, larvae, and pelagic juvenile stages.—No information is available on eggs or larvae. The smallest specimen available is 4.5 mm and is in very poor condition. The fish is almost completely round (inflated?); the spines are short (ca. 0.25 mm) and of uniform length over most of the body. By 13 mm the frontal and pectoral axil spines are ca. 2.5 mm—noticeably longer than the rest of the spines. In the smallest specimen the spines are all erect and the bases resemble small tripods; they may well be fixed at this stage. However, by 8.5 mm the spines are erectile and the fish is definitely capable of inflation. In the 4.5-mm specimen the fin rays are fully formed, as are the nostrils.

The fins remain unpigmented until at least 30 mm except for a small dusky area at the pectoral fin base which forms by 13 mm. In both dorsal and caudal fins, spots gradually spread over the fin from the base. The first row of pectoral fin spots form by 100 mm and the second at about 150 mm. The smallest fish are uniformly dark to medium brown dorsally with a light area at the base of each spine due to the unpigmented spine sheath. Laterally, distinct black spots (0.25-0.50 mm in diameter) are found. These continue across the white ventral surface. By 8.5 mm the white area at the spine bases has disappeared and spots similar to those on the ventral surface have developed on the dorsal surfaces. The spots are now ca. 1 mm in diameter. The ventral spotting is less conspicuous due to the loss of individual spots by 13 mm, and by 20 mm the belly is white and devoid of spots. The dorsal and lateral spots persist and become associated with the spine bases by 100 mm.

Syntypes.—MNHN 2153, two specimens (101 and 108 mm) taken (apparently speared) in the Pacific between Guayaquil and Hawaii.

Distribution.—*Diodon eydouxii* is a pelagic, oceanic species which is found circumtropically (Figure 8) and seems particularly abundant in the eastern Pacific, but this may be an artifact of collecting effort.

Remarks.—In Brissout de Barneville's (1946:142) description, the total mention of *Diodon eydouxii* is as follows: "Mentionnons encore le *Diodon Eydouxii*, Souleyet (Bibron, Coll. Mus. Paris, et Monographie inedite des Diodoniens) remarquable par ses nageoires dorsale et anale subfalciformes." As noted by Brissout de Barneville, Bibron in his unpublished manuscript (MNHN Library MS#867) cited Souleyet as the author of this species. However, Souleyet, insofar as I can determine, never published anything regarding this species. In fact, Bibron's (MS, p. 96) citation refers to the "Voyage de la Bonite. Zool. p . . . . ," i.e., he gave no page number, as if in anticipation of publication by Souleyet. There is no mention of *D. eydouxii* in "Voyage de la Bonite" (Eydoux and Souleyet 1841). Because Brissout de Barneville was the first person to use this name in a published work and because he included descriptive information—albeit limited, *Diodon eydouxii* should be attributed to him.

Kaup's (1855) description of *D. melanopsis* is inadequate, but one of his syntypes (BMNH 1852.3.2.7) is extant. Information provided by A. C. Wheeler (pers. commun., BMNH, 29 October 1975) is sufficient to place *D. melanopsis* in the synonomy of *D. eydouxii*. Günther (1870) incorrectly placed *D. melanopsis* in synonomy with *D.*

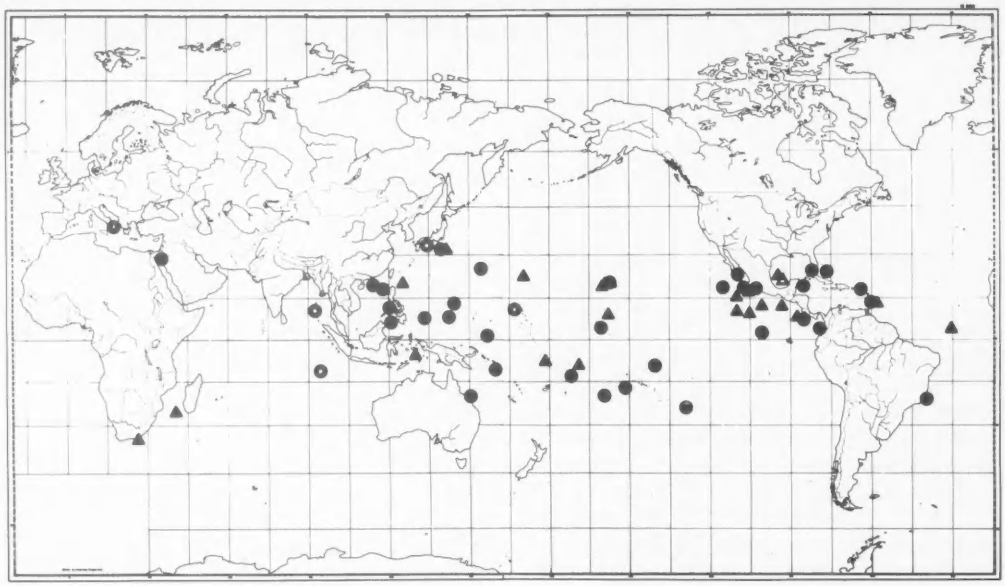

FIGURE 8.—Distribution of *Diodon eydouxii* (triangles) and *Diodon hystrix* (circles). Solid symbols denote specimens examined by me; hollow symbols denote acceptable literature records, photographs, or specimens examined for me by colleagues. Some overlapping records omitted.

spinosissimus Cuvier (see discussion under *D. hystrix*). Le Danois (1959), without comment, incorrectly placed *D. eydouxii* in synonomy with *D. holocanthus*.

The above citations, and those of Troschel (1847) and Duméril (1855) which were essentially reviews of Brissout de Barneville's 1846 paper, constitute the entire literature on *D. eydouxii*.

Diodon eydouxii has undoubtedly been confused in the past with the similar *D. hystrix*. Adaptations to pelagic life by *D. eydouxii* include a lighter, smaller, and more fusiform body compared with *D. hystrix*. The blue color and falcate dorsal and anal fins are also probable adaptations to the pelagic environment. Aside from these characters, *D. eydouxii* differs from *D. hystrix* primarily in its higher dorsal and anal fin ray counts and lower pectoral fin ray counts. *Diodon hystrix* juveniles are pelagic up to a rather large size, and it is tempting to speculate that *D. eydouxii* evolved from this pelagic phase.

All captures of *D. eydouxii* have been at sea (except for one found dead in a South African harbor). Most captures were made under night-lights, and field notes occasionally mention large schools of *Diodon* under the light. Occasional (mostly small) specimens have been taken in plankton, neuston, or midwater trawl hauls.

As a pelagic member of an otherwise slow-swimming, inshore family apparently specialized to feed on heavy-shelled reef animals (e.g., Randall 1967; Hobson 1974), *D. eydouxii* is unusual. However, a well-developed but relatively unspecialized pelagic stage is present at least in *D. hystrix* and *D. holocanthus*. The tetraodontiform fishes, none of which are noted for a combination of rapid and sustained swimming ability and many of which are specialized for feeding on heavy-shelled benthic invertebrates, have a number of pelagic representatives, e.g., *Lagocephalus lagocephalus* (Tetraodontidae) and *Canthidermis maculatus* (Balistidae). In addition, many other species of Tetraodontiformes have pelagic juvenile stages of moderate to long duration. At least 16 of the 22 tetraodontiform genera known to occur in Hawaii, e.g., have an extended pelagic life history stage (no information is available for the other six genera—pers. observ.). The extremely specialized Molidae, a totally pelagic tetraodontiform family, have retained a beaklike jaw structure similar to that of diodontids and tetraodontids. The utility of such jaws in the pelagic environment where the

external shells and exoskeletons of invertebrates are, in general, greatly reduced is difficult to understand.

The stomach contents of three *D. eydouxii* were examined. The two Pacific specimens (BPBM 10551 and NMFS H CHG55-71) examined had fed on a wide variety of large zooplankton: amphipods, crab zoeae, sergestid shrimps, and fish larvae (*Ranzania laevis*, *Acanthocybium solandri*, and a myctophid were identifiable). The Atlantic specimen (ANSP 138122) had eaten approximately 23 small (25-30 mm) fish of the genus *Polydactylus*; these were in a moderately advanced state of digestion.

Material examined.—52 specimens, 4.5-252 mm. EASTERN PACIFIC: MNHN 2153 (2:101-108), between Guayaquil and Hawaii; SIO 69-394 (1:13) 15°N, 110°W; SIO 69-483 (1:40) 19°36′N, 105°16′W; SIO 64-176 (1:138) 13°30.9′N, 92°02.2′W; SIO H52-346 (1:121) 13°11′N, 102°07′W; SIO 64-174 (1:151) 10°01′N, 115°55′W; SIO 64-213 (1:132) 08°24′N, 87°37′W; SIO 73-348 (1:148) 10°25′N, 108°50′W; SIO H52-422 (3:118-131) 11°00′N, 105°29′W. CENTRAL PACIFIC: NMFS H CHG55-71(7:125-147) 11°11′S, 179°13′E; SIO 68-480 (5:100-115) 22°02.8′N, 171°34.0′E; BPBM 10551 (1:143) 12°20′S, 169°44′W; NMFS H TC32-32,34,36, & 47 (4:14.5-26.0) 21°59′N, 158°29′W; NMFS H TC32-66,70,71,73 (6:4.5-17.0) 19°31′N, 156°06′W; SIO 60-264 (3:33-165) 7°53′N, 157°29′W; SIO uncat. *Climax II* (4:144-177) between 25°S-30°N along 155°W. WESTERN PACIFIC: AMS I.B. 2746-7 (2:156-168) 5°21′S, 131°17′E; SIO 61-551 (1:153) 20°35.6′N, 126°33.2′E; SIO 73-106 (2:10) 33°17′N, 138°08′E. INDIAN OCEAN: RUSI 3712 (1:252) Pt. Elizabeth, South Africa; LACM 30138-1 (1:145) 27°41′S, 33°22′E. ATLANTIC OCEAN: SIO 63-565 (1:29) 03°21′N, 30°51′W; NMFS M ORII 39-01 (1:ca. 27) 13°00′N, 60°00′W; ANSP 138122 (1:166) 19°28.8′N, 95°27′W; TU 16864 (1:147) 19°35′N, 95°28′W; TU 12766 (1:152) 20°45′N, 93°15′W. NO DATA: SIO uncat. (1:176).

DIODON HYSTRIX LINNAEUS

Porcupinefish (Figure 9)

Diodon hystrix Linnaeus 1758:335 ("Habitat in India") after Artedi 1738; Bloch 1785:68-73, pl. 126 (American seas); Günther 1870:306, 1910:474 (worldwide); Klunzinger 1871:647-648 (Red Sea); Day 1878:708, pl. 179 (Andaman Is.); Herre 1924:504-505 (Philippine Is.); Meek and Hildebrand 1928:827-829 (Panama; largest specimen only); Le Danois 1959:229-230 (worldwide); de Beaufort 1962:412-413 (East Indies).

Diodon atinga (not of Linnaeus): Bloch 1785:67-69, pl. 125 (American seas); Lacepède 1798:1, 3, pl. 25 (no locality given); Kaup 1855:227 (East and West Indies).

?*Diodon plumierii*? Lacepède 1798:10, pl. 30 (tropical eastern America).

Diodon brachiatus Bloch and Schneider 1801:513 (no locality given).

Diodon punctatus Cuvier 1818:132-133 (no locality given).

Diodon spinosissimus Cuvier 1818:134-135 (Brazil).

Paradiodon hystrix Bleeker 1865:56-57, pl. 207 (East Indies).

Diodon hystrix var. *hystrix* Eigenmann 1885:298-306 (American seas).

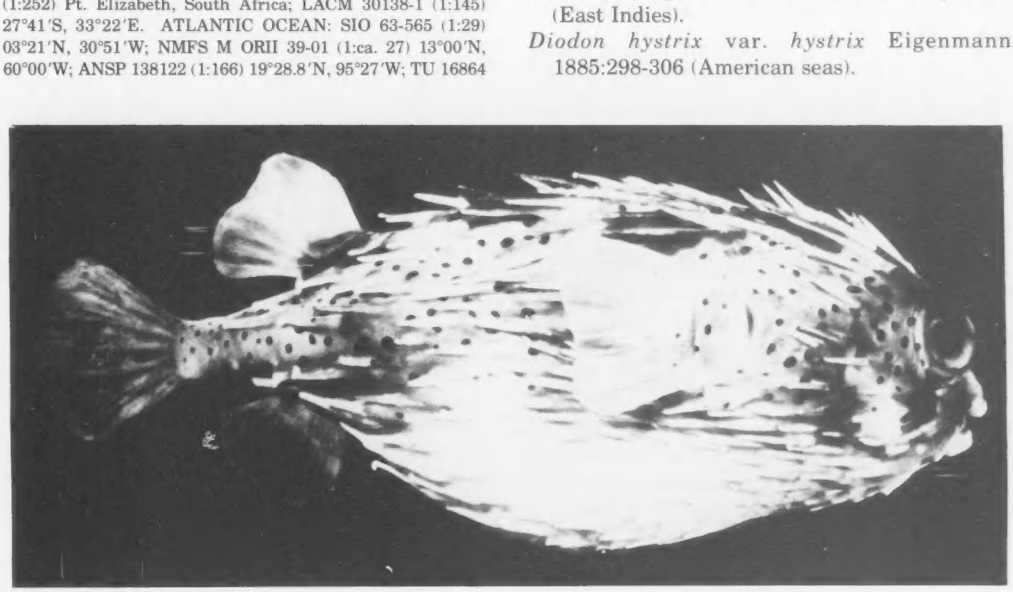

FIGURE 9.—*Diodon hystrix*, 273 mm SL, Oahu, Hawaiian Islands (BPBM 11656). Photo by J. E. Randall.

Diodon nudifrons Jenkins 1904:488-489 (Hawaii).
Diodon armillatus Whitley 1933:107-108, pl. 12, 15 (Australia).
Diodon totara Curtiss 1938:132-133 (Tahiti).

Diagnosis.—A slender-bodied *Diodon*, head width 0.29-0.42, peduncle length 0.14-0.21. Caudal peduncle armed dorsally with short spines. Body spines short to long, slender, and numerous. S-D spines 15-19, S-A spines 14-19. Pectoral axil spines 0.13-0.19, longest on body. A short, fixed tribase spine immediately above gill opening. D 14-17, A 14-16, P 21-25. Nasal tentacle with a pair of lateral openings. No barbels or fleshy tentacles on body. No short, downward-pointing spine below the anterior border of the eye. Dorsal and anal fins rounded. Color pattern dominated by small (<pupil) dark spots dorsally and laterally, these extend onto all fins in adults. A dark gular band starting below the eyes and continuing under the lower jaw, often with a branch extending dorsally between eye and gill opening.

Description.—(34 specimens) D 14-17, A 14-16, the first two rays in each unbranched; P 21-25. Head width 0.29-0.42 ($\bar{x}$ = 0.33; SD = 0.03), body width 0.30-0.51 ($\bar{x}$ = 0.37; SD = 0.04), peduncle length 0.14-0.21 ($\bar{x}$ = 0.17; SD = 0.02), eye 0.05-0.14 ($\bar{x}$ = 0.08; SD = 0.02). Dorsal and anal fins rounded. Nasal tentacles with a pair of lateral openings.

S-D spines 15-19, S-A spines 14-19, about 15 spine rows over the dorsum between pectoral fin bases, about 25 spine rows over the ventrum between pectoral fin bases. Five frontal spines. Longest frontal spine 0.06-0.12 ($\bar{x}$ = 0.09; SD = 0.02), pectoral axil spines 0.13-0.19 ($\bar{x}$ = 0.15; SD = 0.02). Pectoral axil spines the longest on the body, 0.45-0.78 ($\bar{x}$ = 0.58; SD = 0.09) in frontal spines. Spines short to long, and slender. Dorsal spines, other than those dorsolateral spines from over the eye to over pectoral fin, are approximately equal and of about the same length as the ventral spines. The dorsolateral spines immediately above the pectoral fin may be nearly as long as pectoral axil spines. Spines on peduncle short (ca. 2 in frontal spine) and shaft extension not very large (ca. 2.5 in shaft). Shaft extension on other spines reduced, never more than 16% of shaft length. Subdermal bases moderate to very long. In ventral and lateral spines the bases may be 1.5× or more the length of the shaft. In an ovoid area extending from the interorbital to the occipit the spines may be greatly reduced or even embedded, particularly in large individuals. Caudal peduncle with one to three dorsolateral pairs of relatively small spines and one or more unpaired spines located either medially or dorsolaterally. Usually one or two ventrolateral spines on peduncle. A short, fixed tribase spine immediately above the gill opening and a second slightly posterior to it (above the pectoral base), both may be embedded. Three short, flat spines with broad lateral bases form the anterior border of the gill opening. No snout spine.

No barbels or fleshy tentacles.

Dorsally in preserved specimens, the ground color is light grey to dark tan grading to white ventrally. Dorsal and lateral surfaces marked with dark brown to black round spots (<pupil). The spots not generally associated with spine axils. Fins unspotted in small specimens (<50 mm), but all fins become covered with spots in adults. The anal fin is not marked except by a dusky area at its base, and in very large individuals by spots.

A dark gular band extends from the eye down and forward generally paralleling the ventral outline of the lower jaw. Often a branch of this band extends dorsally between the eye and gill opening. These bands may be absent in pelagic specimens.

In life the coloration is essentially as described above, but there may be dorsal blotches (similar to those of *D. holocanthus*). These blotches can rapidly appear and disappear. The blotches are particularly evident during feeding but disappear immediately if the fish is disturbed, e.g., by the approach of a diver. I have never seen these blotches retained in a preserved specimen (for examples of these blotches see Clark and Gohar 1953 and Bagnis et al. 1972:225).

The largest specimen examined was 571 mm, but much larger examples have been reported (e.g., 900 mm, de Beaufort 1962).

Eggs, larvae, and pelagic juvenile stages.—The identification of the eggs and larvae described here as *D. hystrix* is tentative because the larvae have not been reared through metamorphosis. Identification is based on the close similarity of these eggs and larvae to those of *D. holocanthus* and the fact that *D. hystrix* and *D. holocanthus* are the only diodontids that commonly occur inshore in Hawaiian waters. *Diodon eydouxii* has not been taken closer than 30 mi from shore around Hawaii, and *Chilomycterus affinis* is very rare

(pers. observ.; J. E. Randall, pers. commun.). The material available for descriptive purposes is limited, 20 eggs (Figure 10) and 7 larvae.

The eggs of *D. hystrix* are similar to those of *D. holocanthus* (see section on the latter species for characters useful in distinguishing the two types of eggs). *Diodon hystrix* eggs are pelagic, spherical, and 1.9-2.1 mm in diameter ($\bar{x}$ = 2.01; SD = 0.06; n = 20) with 30-50 yellowish oil droplets of 0.03-0.15 mm in diameter. The incubation period is about 5 days at 25°C, but hatching occurs at the end of the late stage (i.e., there is no 'final' stage as defined by Leis 1977; see section on development of *D. holocanthus* for comparison and definition of stages); otherwise, these eggs are similar to *D. holocanthus* eggs.

Development is generally similar to *D. holocanthus* and, aside from hatching at the end of the late stage (i.e., before full eye pigmentation), the only substantive difference is the pigment. Early in the late stage, orange and, to a lesser extent, red chromatophores develop on the dermal sac. The oil droplets tend to be more scattered in *D. hystrix* eggs than they are in *D. holocanthus*. Watson and Leis (1974) illustrated a late stage *D. hystrix* egg (figure A21, p. 115) identified as diodontid II.

The newly hatched larvae of *D. hystrix*, ca. 2.6 mm SL (Figure 11), have only slight eye pigment, an open but apparently nonfunctional mouth, and a large amount of yolk. The eyes become fully pigmented by the second day when the mouth apparently becomes functional. The oldest *D. hystrix* larvae available is a 5-day-old individual of 2.60 mm SL. Aside from some shrinkage during the first 2 days after hatching, development is similar to *D. holocanthus*. Table 3 summarizes morphometric data for the larvae.

Melanophores are sparse at hatching, but soon become abundant dorsally and, except for a more caudad extension of melanophores on the caudal peduncle, pigment is essentially the same as that of *D. holocanthus*. The larvae are orange, rather than the yellow background of *D. holocanthus*.

The eggs and larvae described by Sanzo (1930) and tentatively attributed by him to *Crayracion* sp. (Tetraodontidae) closely resemble those here identified as *D. hystrix*. These specimens were clearly not tetraodontids; marine tetraodontids apparently spawn demersal eggs (Breder and Rosen 1966) and their larvae do not resemble those illustrated by Sanzo (pers. observ.). The eggs studied by Sanzo were larger (2.4 mm) and hatched in a shorter period (3 days at 25°C) than *D. hystrix* eggs, but in all other respects they were similar. It is not known how many species of

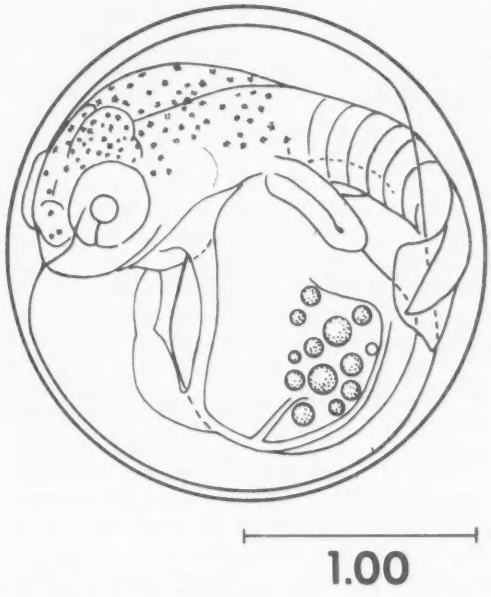

FIGURE 10.—Egg tentatively identified as *Diodon hystrix* just prior to hatching. After Watson and Leis (1974), scale in millimeters.

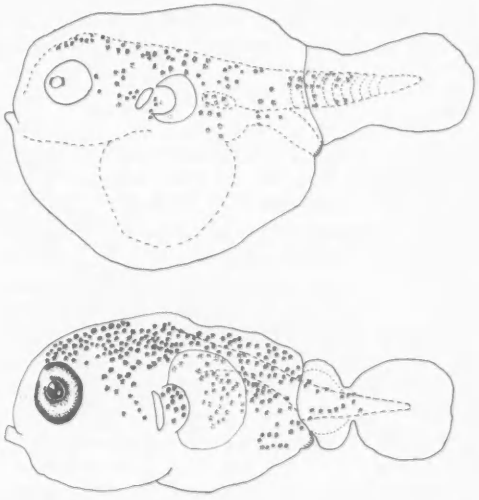

FIGURE 11.—Reared larvae tentatively identified as *Diodon hystrix*: (top) newly hatched larva, 2.57 mm SL, and (bottom) 5-day-old larva, 2.60 mm SL. Hawaiian material.

TABLE 3.—Morphometric and meristic data for larval and juvenile *Diodon hystrix* (measurements in mm). ? indicates individuals of unknown age caught in plankton samples; × indicates damaged.

Age (days) of reared fish	Notochord or standard length	Snout to anus length	Width of eye	Head length	Head width	Mouth width	Fin ray counts		
							D	A	P
Larvae:									
1	2.6	2.0	0.3	0.9	1.0	0.4	0	0	0
3	2.1	1.7	0.3	0.8	1.1	0.7	0	0	0
?	2.4	1.7	0.4	0.9	1.4	0.5	0	0	0
?	2.4	1.9	0.4	1.0	1.5	0.7	0	0	0
?	2.4	1.8	0.3	0.8	1.3	0.5	0	0	0
?	2.4	1.8	0.4	0.8	1.4	0.7	0	0	0
5	2.6	1.8	0.4	0.9	1.2	0.7	0	0	0
Juveniles:									
?	5.1	4.5	1.0	1.6	3.2	1.1	×	×	23
?	11.1	9.0	2.1	5.1	7.0	2.5	15	15	22

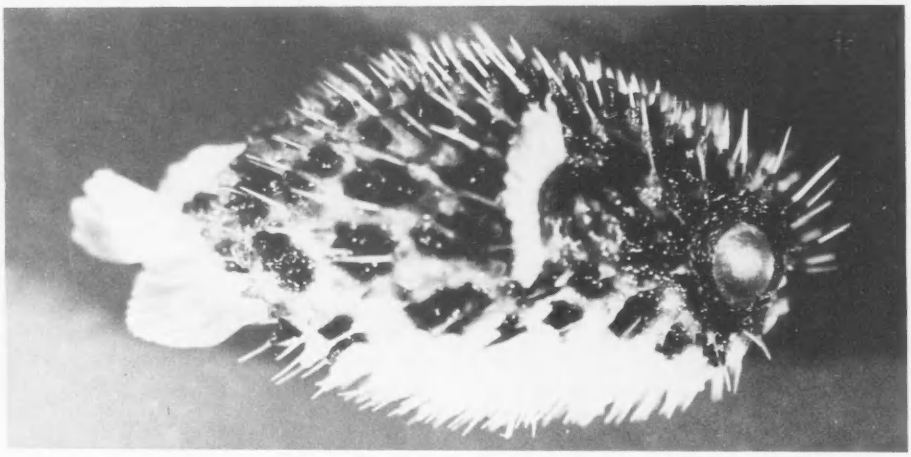

FIGURE 12.—Pelagic juvenile of *Diodon hystrix*, 26 mm SL, western Atlantic (NMFS M *Oregon II* 72-39-36).

Diodon occur in the Red Sea where Sanzo obtained his specimens; only *D. hystrix* is reported to occur there (e.g., Clark and Gohar 1953).

Metamorphosis to the spiny juvenile stage occurs before 5 mm SL. Juveniles of *D. hystrix* are similar in shape, development, and pigmentation to *D. holocanthus* except that the spines of the former are shorter and its snout is more heavily pigmented (Figure 12). *Diodon hystrix* juveniles remain pelagic for an unknown time, but the largest pelagic individual seen was 180 mm while the smallest individual taken inshore was 191 mm.

Holotype.—No holotype or type-series is known to exist. Linnaeus based his description on that of Artedi (1738).

Distribution.—*Diodon hystrix* is found circumtropically (Figure 8) and often in temperate areas, especially in the western boundary currents. This species apparently is the only member of the genus in the Mediterranean (Torchio 1963).

Remarks.—Linnaeus provided very little diagnostic data in his brief description, the useful information consisting of a mention of long spines, chiefly on the sides. This could apply to *D. hystrix*, as described above, *D. liturosus*, or *D. eydouxii*. Bloch (1785) was the first to use recognizably the name *hystrix*. His illustration of "*D. hystrix*" is clearly of the species here considered as *D. hystrix*.

Several authors have incorrectly applied the name *Diodon atinga* Linnaeus to this species (see synonomy), but it is clear from the original de-

scription that *D. atinga* is a *Chilomycterus* (sensu lato).

Diodon plumierii Lacepède is included in the synonomy of *D. hystrix* with some doubt. The description is not very helpful, but the illustration by Plumier (Lacepède 1790, plate 30), while not immediately recognizable as *D. hystrix*, is probably of that species. The relatively elongate body, short spines, and the three spines on the dorsal surface of the peduncle all indicate *D. hystrix*. The description stated that the fish was blue with white spots; this coloration is not found in any known species of *Diodon*. Lacepède's description was based solely on Plumier's illustration.

Diodonnbrachiatus Bloch and Schneider is based at least in part on the "Erizo" of Parra (1787) whose illustration is clearly of *D. hystrix*.

Cuvier's *D. punctatus* is attributable to *D. hystrix* on the basis of his description, and examination of the syntypes (MNHN A.8369, A.8373, and A.8367) by M.L. Bauchot (pers. commun. MNHN, 20 May 1975).

Diodon spinosissimus Cuvier has been a source of confusion. This stems at least in part from the presence of two species in Cuvier's syntypic series (M. L. Bauchot, pers. commun., MNHN, 20 May 1975). The larger specimen (MNHN B.1294) is a *D. hystrix* from Brazil, while the smaller syntype (MNHN B.1294) is a *D. liturosus* from Vanikoro, Santa Cruz Islands, in the western Pacific. Le Danois (1961) referred to the above specimen of *D. hystrix* as the holotype, while there is no evidence that Cuvier recognized it as such, I follow Le Danois' lead and designate MNHN B.1294 as the lectotype of *D. spinossisimus*.

Since the publication of Günther (1870), relative unanimity has prevailed, with most authors applying only the name *D. hystrix* to this species. The three exceptions, barring misidentification of *D. holocanthus*, are *D. nudifrons* Jenkins, *D. armillatus* Whitley, and *D. totara* Curtiss. These are easily referred to *D. hystrix* solely on the basis of the published descriptions (S. Karnella, pers. commun., USNM, 28 January 1976, reports that Jenkins' holotype cannot be located at USNM even though it was cataloged as USNM 50854).

The apparent long pelagic stage of *D. hystrix* has undoubtedly contributed to its wide distribution and to the relative uniformity among populations (Table 1).

Little is known of the ecology of *D. hystrix*. Randall (1967) and Hobson (1974) gave information on feeding and diel activity patterns. *Diodon hystrix* is a nocturnal predator on hard-shelled invertebrates such as gastropods, hermit crabs, and sea urchins. Eger (1963) reported toxic dermal secretions in *D. hystrix*. This species is eaten by people in Hawaii (pers. observ.) and Tahiti (Curtiss 1938; Bagnis et al. 1972) without apparent ill effect, although it is frequently classified as poisonous (e.g., Halstead 1967).

Material examined.—43 specimens, 5.5-571 mm. EASTERN PACIFIC: SIO 64-214 (1:128) 7°47′N, 85°45′W; SIO H52-415 (1:180) 2°50.5′N, 101°28′W; UA 73-83-21 (1:236) Cabo San Lucas, Baja California Sur, Mexico; UA 68-59-11 1:199) Punta Mal Paso, Manta, Ecuador; CAS 1244 (1:209) Clarion I., Revillagigedos; CAS H46-241 (2:191-202) Acapulco, Guerrero, Mexico; CAS uncat. (1:215) La Paz, Baja California Sur, Mexico; NMFS LJ N-49, 67-2 (1:5.5) 18°N, 107°W. CENTRAL and WESTERN PACIFIC: HAWAIIAN IS.—HIMB (1:311) Kaneohe Bay, Oahu; NMFS H-243 (1:135) off Kailua, Hawaii; NMFS H-241 (1:142) 10 mi. W. Keahole Pt., Hawaii; BPBM 11656 (1:272.5) Moku Mana, Oahu. LINE IS.—BPBM 9798 (1:338) Washington I. MARQUESAS IS.—BPBM 12139 (1:290) Nuku Hiva. PITCAIRN I.—BPBM 16821 (1:278), 16717 (1:282). SOCIETY IS.—GVF stn 22 (1:211) Maiao I. COOK IS.—GVF M-37 (1:327) Mangaia I. MARCUS I.—BPBM 8403 (1:403). MARIANA IS.—BPBM 5122 (1:200) Guam. SOLOMON IS.—CAS 6003 (1:107) Bellona I. CAROLINE IS.—GVF stn 29 (1:258) Ifaluk Atoll; GVF stn 12 (1:220) Palau Is.; GVF 176 (1:571) Kapingamarangi Atoll. PHILIPPINE IS.: CAS 26419 (1:199) Jolo I.; CAS 26418 (1:286) Culion I. SOUTH CHINA SEA: SIO 70-342 (1:49.5) 18°14.4′N, 119°45.2′E; GVF 1748 (1:196) 20°46′N, 116°53′W. JAPANESE WATERS: SIO 73-106 (1:ca. 10) 33°17′N, 138°08′E. AUSTRALIA: AMS IA.6105 (1:263) Hayman I., Queensland. INDIAN OCEAN: RED SEA—CAS HV-1661 (1:235) Eylath, Gulf of Aqaba. WESTERN ATLANTIC: CAS BMN-7526 (1:465) Vitória, Brazil; CAS 23805 (1:307) Harbour I., Bahamas; GCRL V66:1703 (1:328) St. Thomas, Virgin Is.; CAS 19210 (1:335) Key West, Fla., USA; NMFS M *Bowers* 1-10 (1:29.2) 26°00′N, 70°30′W; NMFS M *Oregon II* 72-39-58 (1:30.0) 21°01′N, 80°14′W; NMFS M *Oregon II* 72-43-146 (2:16.0-18.9) Caribbean; NMFS M *Oregon II* 72-39-36 (1:26.2) 17°08′N, 69°58′W; NMFS M *Oregon II* 72-39-136 (1:25.0) 23°45′N, 84°20′W; NMFS M *Oregon II* 76-66-19791 (1:40.0) 17°50′N, 74°47′W.

In addition, a number of specimens (CAS, NMFS M, material) were identified, but not examined in detail. These fish form the basis for some of the points plotted in Figure 8.

DIODON NICTHEMERUS CUVIER

Globefish (Figures 4, 13)

Diodon nicthemerus Cuvier 1818:135 pl. 2 (Australia).

Diodon nycthemerus: Kaup 1855:228 (no locality given).

Diodon nichtemerus: Duméril 1855:278 (no locality given).

Atopomychterus nychthemerus: Günther 1870:315 (South Australia, Tasmania).
Diodon spinossisimus (not of Cuvier): Castelnau 1872:290 (Australia).
?*Diodon blochii*? Castelnau 1872:210 (Australia).
Atopomychterus nichthemerus: Waite 1923:229 (South Australia, Tasmania).
Dicotylichthys nychthemerus: Fraser-Brunner 1943:17 (Australia).
Atopomycterus nicthemerus: Scott 1957:154 (Tasmania).
Diodon nycthemerus: Le Danois 1959:227 (Australia).
Atopomycterus nicthemerus: Scott 1962:299 (West Australia, South Australia, Tasmania).

Diagnosis.—Round-bodied *Diodon*, head width 0.34-0.43, peduncle length 0.12-0.16. Caudal peduncle without spines. Body spines long and narrow, but relatively few in number, S-D spines 9-12, S-A spines 10-11. Pectoral axil spines shorter than longest frontal spines. No short, fixed tribase spine immediately above gill opening. Fin ray counts low, D 12-13, A 12-14, P 19-21. Nasal tentacle with a pair of lateral openings which are separated by a thin membrane; this is often absent (more often in larger individuals) resulting in the nostrils appearing "confluent, each nasal organ appearing as a bifid tentacle" (Fraser-Bruner 1943:16). Fins without dark spots. Individuals 100 mm and greater with four dark bars on the sides and lacking dark spots on the body.

Description.—(10 specimens) D 12-13, the first unsegmented; A 12-14, the first unsegmented; P 19-21; vertebrae 9 + 12 = 21 (Günther 1870). Head width 0.34-0.43 ($\bar{x}$ = 0.39; SD = 0.03), body width 0.39 - 0.52 ($\bar{x}$ = 0.45; SD = 0.05), peduncle length 0.12-0.16 ($\bar{x}$ = 0.14; SD = 0.01), eye 0.09-0.17 ($\bar{x}$ = 0.12; SD = 0.02) greatest in smaller specimens. Dorsal, anal, and caudal fins all rounded, middle rays longest. Nasal tentacles with a pair of lateral openings which are separated by a thin membrane which is often broken or resorbed, especially in larger individuals, resulting in the nasal organ appearing as a bifid tentacle.

S-D spines 9-12, S-A spines 10-11, about 9 spine rows over dorsum between pectoral fin bases, about 15 spine rows over ventrum between pectoral fin bases. Five frontal spines. Longest frontal spines 0.15-0.23 ($\bar{x}$ = 0.19; SD = 0.03), greatest in smaller specimens, pectoral axil spines 0.11-0.20 ($\bar{x}$ = 0.15; SD = 0.03). Frontal spines longest on body; 1.12-1.35 ($\bar{x}$ = 1.25; SD = 0.08) times pectoral axil spines, although many dorsal spines nearly as long. Ventral spines shorter than dorsal spines (ca. 1.4 in dorsal spines). Lateral spines

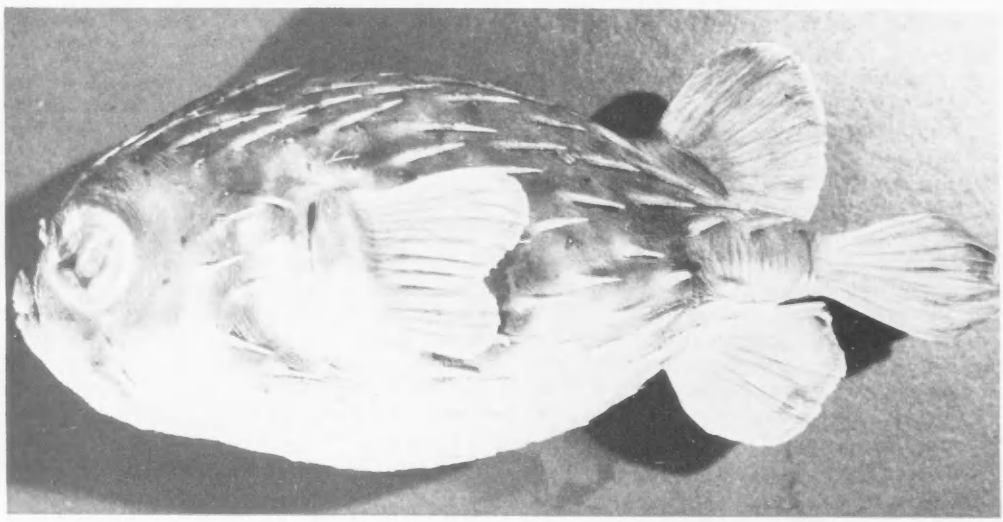

FIGURE 13.—*Diodon nicthemerus*, 110 mm SL, Victoria, Australia (AMS I.16990-004).

nearly as long as dorsal spines (ca. 1.2 in dorsal spines). Spines long and narrow. Subdermal lateral bases short (1.5-5 in shaft length) and the shaft extension reduced or lacking. No spines on caudal peduncle, but along base of both dorsal and anal fins there is a spine whose shaft extends onto the peduncle. No short fixed spine with three subdermal bases immediately above the gill opening. One or two spines originating between eye and gill opening which extend over the depression surrounding the gill opening. No spines on the snout, but a broad spineless area around the eye. Aside from nasal organs, no barbels or tentacles.

Upper parts in preserved specimens uniformly dark brown to grey with four dark bands descending onto the sides: the first below the eye, the second between the eye and gill opening, the third behind pectoral fin, and the fourth below dorsal fin. The first two bars are swept back and the third swept forward. The second and third bars sometimes meet below the pectoral fin to form a ring about its base and the gill opening. White to light grey below a level even with the mouth (except the bars) with no ventral spotting. Fins somewhat dusky but unspotted. In specimens of about 100 mm the uniformly dark dorsum is broken up into large blotches which appear as continuations of the lateral bars. In smaller fish the dorsal blotches are broken up into small diffuse dark spots (ca. one-half of eye diameter); some of the spots in association with spine bases. Belly is unspotted at all sizes. Le Danois (1959) stated that the bars become lighter in color in large specimens.

Scott (1962:299) gave the following information on live coloration: greenish indigo above, white to silvery below, four dark bars on the sides with several large yellowish spots incorporated in the bars, fins plain yellowish-green and the spines lemon-yellow. An excellent color photograph was provided by Coleman (1974:99).

The largest specimen examined was 158 mm SL. However, both Le Danois (1959) and Scott (1962) reported specimens of 280 mm. A 111-mm specimen was sexable as a male, but may not have been mature.

Eggs, larvae, and pelagic stages.—No information.

Syntypes.—MNHN B.1313 (75 mm) and MNHN 51 (100 mm) taken by Peron and Lesueur in Australia. M.L. Bauchot examined these specimens and provided notes and photographs. Le Danois

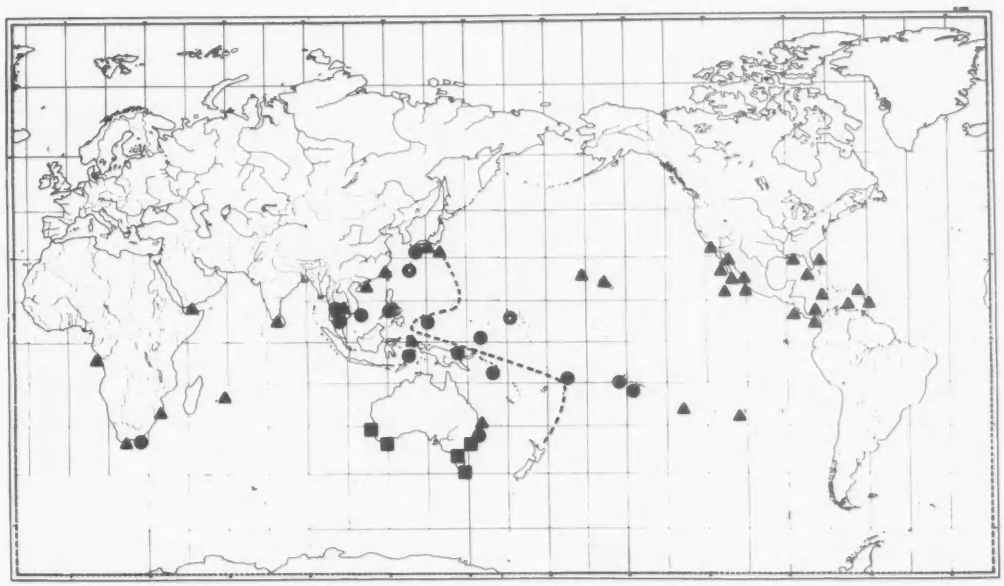

FIGURE 14.—Distribution of *Diodon nicthemerus* (squares), *D. liturosus* (circles), and *D. holocanthus* (triangles). Solid and hollow symbols as in Figure 8. Dashed line indicates position of the Andesite line.

(1961) referred to MNHN B.1313 as the holotype of *D. nichthemerus*. There is no evidence that Cuvier regarded it as such, and I prefer not to regard Le Danois' statement as constituting a lectotype designation.

Distribution.—Apparently confined to the southern half of Australia and Tasmania (Figure 14).

Remarks.—Günther (1870) was the first to place this species in *Atopomycterus*, apparently on the basis of Bleeker's (1865) diagnosis of *A. diversispinus*, the type of the genus, as possessing a bifid nasal tentacle and slender spines with long double roots. However, as indicated above, the double spine roots of *D. nicthemerus* are relatively short and the bifid nasal tentacle is not a consistent character. Bleeker (1865) in the first published usage of the name *Atopomycterus diversispinus*, based his brief description on an unpublished description of a specimen (NMHN 2159) by Verreaux. M. L. Bauchot (pers. commun., MNHN, 23 June 1975) reports that Le Danois (1959) was correct in stating that only the ventral and prepectoral dorsal spines have two bases. The postpectoral dorsal spines are tribased and fixed.

Fraser-Brunner (1943) followed Günther (1870) in placing *D. nicthemerus* in *Atopomycterus* (as a subgenus of *Dictoylichthys*), apparently solely on the basis of the bifid nasal tentacle. Fraser-Brunner and Günther regarded the condition of the nasal tentacle to be of more importance than the character of the spines, but this does not seem tenable to me. Of the 11 specimens of *D. nicthemerus* for which I have data, 6 (41-111 mm) had tubular nostrils on both nasal tentacles, 1 (84 mm) had one tubular and one bifid tentacle, and 4 (100-158 mm) had a pair of bifid nasal tentacles. This indicates that the bifid nasal tentacle is an ontogenetic character that cannot be used in generic classification. The spines of *D. nicthemerus*, aside from their reduced lateral roots and anterior shaft extension, are no different from those of the other species of *Diodon*.

Diodon blochii Castelnau is placed in synonomy with *D. nicthemerus* with some doubt. The type cannot be found in MNHN, AMS or in the National Museum of Victoria, Australia. The description is incomplete and does not fit exactly any of the five species considered here, but of those, it matches *D. nicthemerus* most closely, particularly in meristic characters.

The distribution of *D. nicthemerus* is unusual for a *Diodon* in both its limited range and its location in a temperate rather than tropical area. This limited range might indicate a pelagic stage that is less well developed than that of other members of the genus, but if this species requires a temperate environment it may have colonized all the available habitat within a reasonable dispersal range (although in a personal communication of 4 February 1976, J. Moreland reports that there were no specimens of any *Diodon* sp. in the collections of the National Museum of New Zealand).

Coleman (1974) reported that *D. nicthemerus* inhabits areas of sand or mud bottom and feeds on molluscs, crustaceans, and echinoderms.

Material examined.—Nine specimens, 41-158 mm. All specimens from the Australian Museum: I.13619 (41 mm) Swan R., West Australia; I.12840 (67) Fremantle, West Australia; I.A.629 (78.5) King George's Sound, West Australia; I.16899-003 (84.5) Jervis Bay; I.A.5829 (104) Port Franklin, Victoria; I.16990-004 (110) Port Phillip Bay, Victoria; I.16894-001 (111) Jervis Bay; I.6240 (111) Tamar R., Tasmania; I.17564-001 (158) Snug Beach, Tasmania.

DIODON LITUROSUS SHAW

Short-spine Balloonfish
(Figures 5, 15, 16)

Le Diodon Tacheté Lacepède 1798:13-15 ("New Cythere").

Diodon liturosus Shaw 1804:436 (Indian Seas); Masuda et al. 1975:140, 335 (southern Japan).

Diodon maculatus Duméril 1855:278 (Latinization of Le Diodon Tacheté Lacepède) after Bibron MS.

Paradiodon novemmaculatus (not of Cuvier): Bleeker 1865:57-58, pl. 206 (East Indies).

Diodon maculatus var. B: Günther 1870:308 (East Indies).

Diodon bleekeri Günther 1910:475-476, pl. 179 (Society Is.); Herre 1924:506-507 (Philippine Is.); Orsi 1974:176 (Vietnam).

Diodon holacanthus (not of Linnaeus): de Beaufort 1962:410-412 (Indo-Australian archipelago); Bagnis et al. 1972:227 (French Polynesia).

Dicotylichthys punctulatus (not of Kaup): Grant 1972:472 (Australia).

Diagnosis.—Round-bodied *Diodon*, head width 0.33-0.42, peduncle length 0.12-0.18. Caudal peduncle without spines. Body spines short and

numerous. S-D spines 16-21, S-A spines 17-22. Frontal spines 0.04-0.10, much shorter than pectoral axil spines. A short, fixed tribase spine immediately above gill opening. A short, downward-pointing spine below the front border of eye. Five frontal spines. D 14-16, A 14-16, P 21-25. Nasal tentacle normally with a pair of lateral openings. Usually two small barbels on the chin. A fleshy tentacle may be present over each eye. Color pattern dominated by large, light-edged dorsal, and dorsolateral blotches. The lateral postpectoral surfaces with small spots associated with the spine axils. A dark gular band starting from below the eye and continuing under the chin. Fins without spots except at bases.

Description.—(27 specimens) D 14-16, A 14-16, the first two rays undivided; P 21-25. Head width 0.33-0.42 ($\bar{x}$ = 0.36; SD = 0.03), body width 0.35-0.51 ($\bar{x}$ = 0.41; SD = 0.04); peduncle length 0.12-0.18 ($\bar{x}$ = 0.15; SD = 0.01), eye 0.08-0.15 ($\bar{x}$ = 0.10; SD = 0.02). Dorsal, anal, and caudal fins rounded, middle rays longest. Nasal tentacles normally with a pair of lateral openings; occasionally, the end of the tentacle is split, giving rise to a bifid nasal tentacle without nostrils. When split, the bifid arms tend to become thickened and papillose.

S-D spines 16-21, S-A spines 17-22, about 14 spine rows over the dorsum between pectoral fin bases, about 26 spine rows over the ventrum between pectoral fin bases. Five frontal spines. Longest frontal spine 0.04-0.10 ($\bar{x}$ = 0.07; SD = 0.02), pectoral axil spines 0.10-0.15 ($\bar{x}$ =0.12; SD = 0.01). Pectoral axil spines longest on body, 0.40-0.78 ($\bar{x}$ = 0.61; SD = 0.09) in frontal spines. Spines generally short. The only markedly elongate dorsal spines are those above the pectoral fin (ca. 0.60 in frontal spines). Frontal, middorsal, and lateral (excluding pectoral axil spines) spines all of about the same length. Ventral spines somewhat shorter (ca. 1.3 in frontal spines). The spines of the interorbital region and nape often reduced or buried, especially in individuals larger than 150 mm, but, in any case, shorter than frontal spines. The shaft extension is variably developed, its size positively correlated with the size of the lateral bases. No spines on caudal peduncle, but along the base of both dorsal and anal fins there is a spine whose shaft extends onto the peduncle. In two of the specimens examined these spines were on the peduncle, but they were still clearly associated with the fin bases. A short, fixed tribase spine immediately above the pectoral base. Three short, flat spines with broad lateral bases form the anterior border of the gill opening. A short, downward-pointing spine below the anterior border of the eye.

Two small barbels on the chin. A fleshy tentacle above each eye present in about one-third of the specimens. Rarely, a more extensive set of tentacles along the ventrolateral edge of the body similar to that described for *D. holocanthus*.

Background color in preserved specimens varies from dark brown to light buff. The color pattern is dominated by several large dark brown to black blotches on dorsal and lateral surfaces. These blotches edged in a color lighter than background

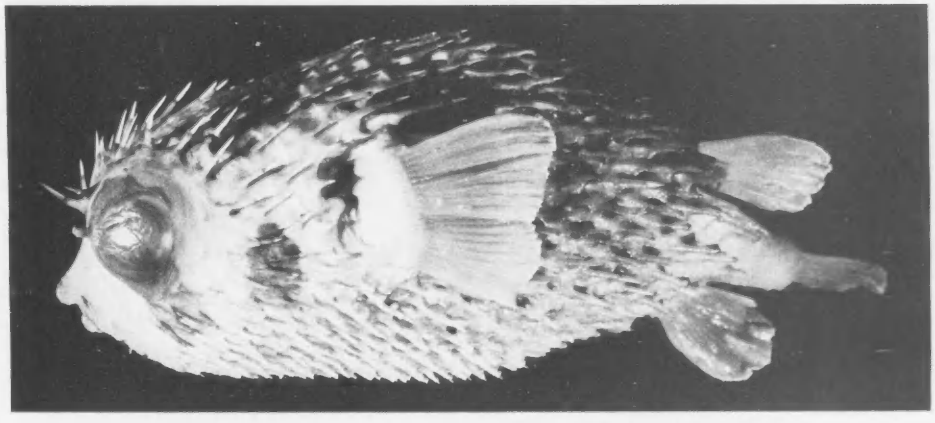

FIGURE 15.—*Diodon liturosus*, 142 mm SL, Ko Samet, Thailand (CAS 30967).

color (usually white). The blotches are located as follows: (Figure 16): 1) one round blotch around the base of the dorsal fin; 2) one round blotch middorsally about midway between the dorsal fin and pectoral base; 3) one round blotch above each pectoral fin along the dorsolateral surface just posterior to the fin base; 4) a broad transverse bar across the occipital region; 5) an irregularly shaped blotch immediately below the occipital blotch, between the eye and pectoral fin; and 6) a bar which crosses each eye downward and usually connects with a broad gular band across the ventral surface just behind the mouth (the bar which crosses the eye does not extend across the interorbital). The chin barbels are located within the gular band, but are light in color. Postpectorally the lateral surfaces are marked with small (<pupil diameter) spots associated with the spine axils. No spots dorsally or ventrally (except in specimens <50 mm). Specimens of 100 mm may be mottled on the caudal peduncle and often have four spots on the iris. Ventrum white and fins unmarked except at bases. A 24.5-mm specimen is light brown dorsally and covered everywhere (except fins) with small (ca. = pupil) dark spots. The spots are less dense on the belly and are not associated with the spine bases. Color in life essentially the same as above but fins yellow.

The largest specimen examined was 349 mm. However, de Beaufort (1962) reported specimens of 500 mm, and Masuda et al. (1975) reported a specimen of 600 mm total length.

Eggs, larvae, and pelagic stages.—No information. However, the 24.5-mm specimen mentioned above which has "pelagic spotting" may be a pelagic juvenile (the collection data are incomplete). The smallest specimen definitely found inshore was 94 mm.

Holotype.—Shaw (1804) based his description on that of Lacepède (1798), who in turn had based his on a manuscript description by Commerson. The fish illustrated by Commerson is apparently lost.

Distribution.—*Diodon liturosus* ranges throughout the Indo-West Pacific (Figure 14) from South Africa to Japan and the Society Islands, but is absent from Hawaii. Areas of overlap with the closely related *D. holocanthus* are along the edges of the Pacific and Indian Oceans.

Remarks.—*Diodon liturosus* usually has been considered a junior synonym of *D. holocanthus* (e.g., Le Danois 1959) but if recognized as a distinct species has generally been called *D. bleekeri*. Shaw's (1804) description is short and based almost totally on color. However, several details clearly indicate which species is involved. The distribution and number of spots, particularly the "two transverse ones, the first situated *beneath* the eye and the second between the eye and pectoral fin" (Shaw 1804:436, emphasis mine), and the "dusky cloud" marking the throat clearly eliminate *D. holocanthus*, and apply only to *D. liturosus* as described above. In addition, Lacepède (1798) gave a pectoral fin ray count of 24 which is rare for *D. holocanthus* (Lacepède did not provide a Latin binomial in his description of Le Diodon Tacheté).

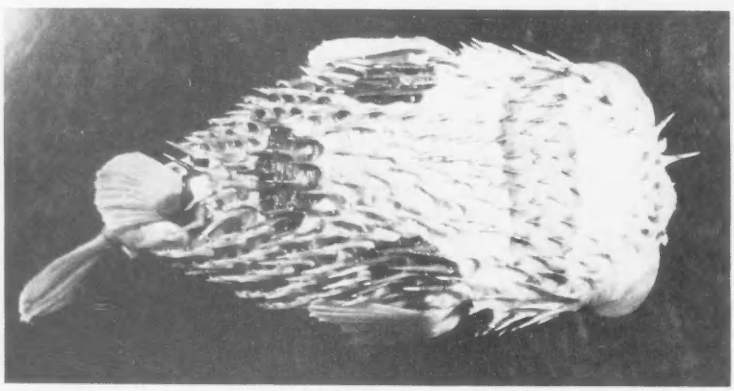

FIGURE 16.—Dorsal view of *Diodon liturosus*, note lack of interorbital bar. Same specimen as in Figure 15.

ERRATA

Fishery Bulletin, Vol. 76, No. 3

Leis, Jeffrey M., "Systematics and zoogeography of the porcupinefishes (*Diodon*, Diodontidae, Tetraodontiformes), with comments on egg and larval development," p. 535-567.

1) Page 545, the photo is mirror image of a photo of *Diodon holocanthus* by J. E. Randall.

2) Page 555, the photo is mirror image of a photo of *Diodon hystrix* by J. E. Randall.

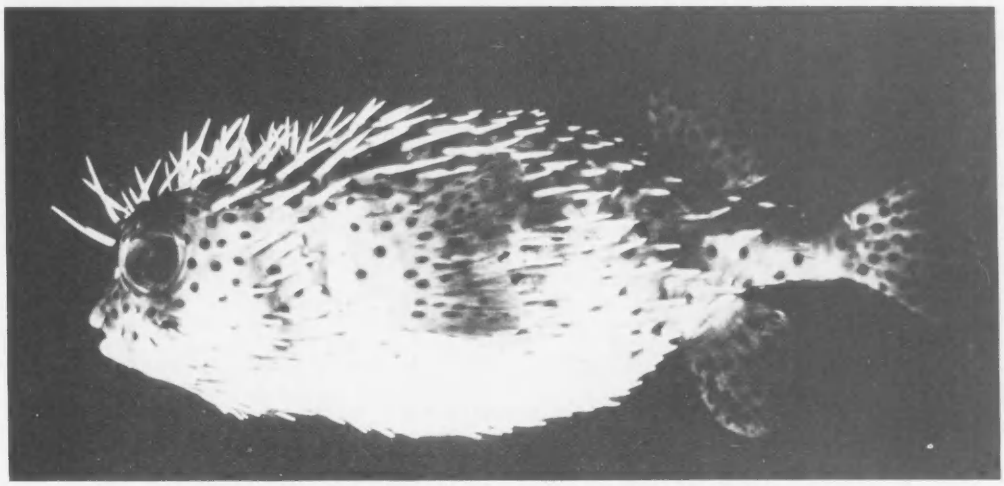

FIGURE 9.—*Diodon hystrix*, 273 mm SL, Oahu, Hawaiian Islands (BPBM 11656). Photo by J. E. Randall.

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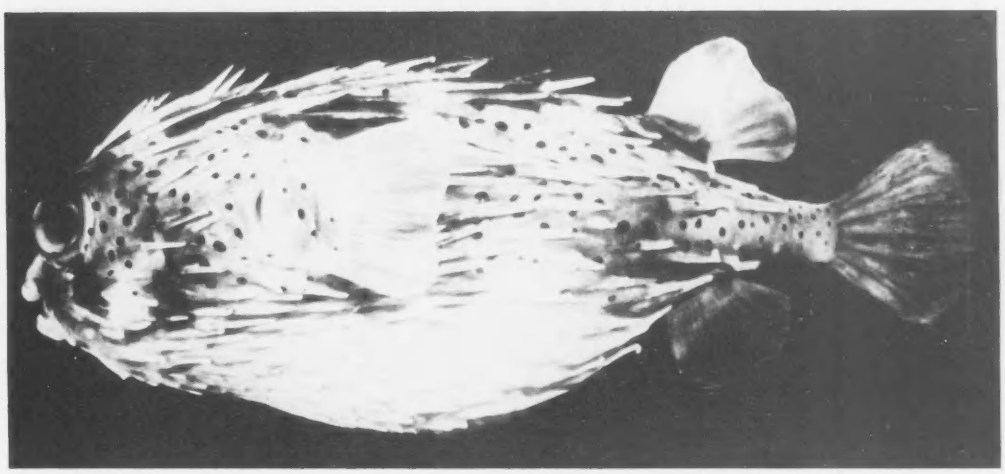

FIGURE 17.—*Diodon holocanthus*, 195 mm SL, Wolmar, Mauritius (BPBM 20255). Photo by J. E. Randall.

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Günther (1910) did not designate a holotype or syntypic series for *D. bleekeri*, but his description, along with the included plate by Garrett, provide sufficient information to synonymize this nominal species with *D. liturosus*.

In large part the confusion between *D. holocanthus* and *D. liturosus* has resulted from the limited geographical overlap in the distributions of these two species. Because comparative material of both species is rarely available from a given area, it is not surprising that these similar species have been confused, especially considering the less than detailed descriptions available.

Nothing is known of the ecology of this species.

Material examined.—30 specimens, 24.5-340 mm. INDIAN OCEAN: RUSI 3707 (1:124) Port Elizabeth, South Africa. AUSTRALIA: AMS B.1349 (1:128) Port Jackson, New South Wales. EAST INDIES: AMS B.7810 (1:114) Malay Archipelago; CAS 28225 (3:105-116) Madang, New Guinea; BPBM 19239 (1:132) Ambon, Molucca Is. PHILIPPINE IS.: CAS 38383 (1:130) Panay. GULF OF THAILAND: CAS 30967 (4:107-162) Ko Samet, Thailand; GVF stn 135 (1:186) Goh Proet I. Thailand; GVF stn 8 (1:201) Goh Kram I. Thailand; GVF 2646 (1:264) Goh Luem I. Thailand; GVF 2067 (4:94-152) Bangkok. JAPAN: CAS 6987 (1:24.5) Misaki. PALAU IS.: GVF stn 57-45 (1:155); GVF stn 61 (2:133-139); GVF stn 57-43 (1:217). KAPINGAMARINGI: GVF stn 51 (1:125). SOLOMON IS.: CAS 6004 (1:123) Bellona I. AMS B.1350 (1:112) Solomon Is. SOCIETY IS.: GVF (no station data) (1:340) Moorea; GVF stn 39 (1:195) Bora Bora; BPBM 8745 (1:313) Tahiti.

DIODON HOLOCANTHUS LINNAEUS

Balloonfish or Spiny Puffer
(Figures 17, 18)

Diodon holocanthus Linnaeus 1758:335 ("Habitat in India") after Artedi 1738; Marshall 1965:500-501, pl. 63 (Queensland, Australia); Orsi 1974:176 (Vietnam).

Diodon pilosus Mitchill 1815:471, pl. 6 (New York); De Kay 1842:326, pl. 55 (New York).

Diodon novemmaculatus Cuvier 1818:136, pl. 6 (no locality given).

Diodon sexmaculatus Cuvier 1818:136-137, pl. 7 (no locality given).

Diodon quadrimaculatus Cuvier 1818:137, pl. 6 (Tahiti? - see text).

Diodon multimaculatus Cuvier 1818:137-138, pl. 7 (no locality given).

?*Diodon maculifer*? Kaup 1855:229 (Cape of Good Hope).

Paradiodon quadrimaculatus: (Bleeker 1865:57-58, pl. 212 (East Indies).

Trichodiodon pilosus: Bleeker 1865:49; Günther 1870:316 (both after Mitchill 1815).

Atopomycterus bocagei Steindachner 1866:447-478, pl. 6 (Port Jackson, Australia).

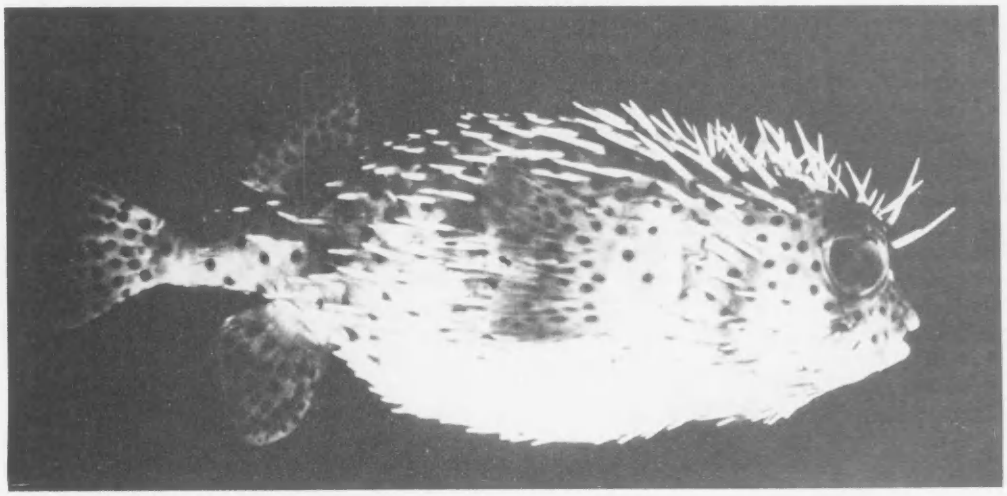

FIGURE 17.—*Diodon holocanthus*, 195 mm SL, Wolmar, Mauritius (BPBM 20255). Photo by J. E. Randall.

Diodon maculatus var. A (not of Lacepède): Günther 1870:307-308, 1910:475 (various localities).

Diodon liturosus (not of Shaw): Jordan and Gilbert 1883:377 (Panama); see Eigenmann (1885) for other references.

Diodon hystrix var. *holocanthus* Eigenmann 1885:298-306 (American seas).

Diodon holacanthus (alternate spelling): Jordan and Evermann 1891:1746 (American seas), 1905:436-437 (Hawaii); Jordan and Snyder 1902:257 (Japan); Herre 1924:505-506 (Philippines); Meek and Hildebrand 1928:829-831 (Panama); Le Danois 1959:231 (in part) (various localities); Randall 1968:282 (Caribbean).

Diodon hystrix (not of Linnaeus): Meek and Hildebrand 1928:827-829 (in part) (Panama); Poll 1959:354-355 (West Africa).

Diagnosis.—Round-bodied *Diodon*, head width 0.26-0.46, peduncle length 0.09-0.20. Caudal peduncle without spines. Body spines rather long, moderate in number. S-D spines 12-16, S-A spines 12-15. Frontal spines 0.13-0.28, from slightly shorter to much longer than pectoral axil spines. A short, fixed tribase spine immediately above the gill opening. A short, downward-pointing spine below the front border of the eye may be present in Atlantic specimens, but is absent in Indo-Pacific specimens. D 13-15, A 13-15, P 21-24. Nasal tentacle with a pair of lateral openings. Two small barbels on chin. On inshore specimens sets of short, fleshy tentacles: one over each eye, a pair in the middle of the back, six along the ventrolateral edge of body, and one on the dorsolateral edge of body posterior to pectoral fin. Some or all of the tentacles often lacking. Color pattern dominated by large dorsal and dorsolateral blotches. Small spots often quite profuse between large blotches. Fins without spots.

Description.—(45 Indo-Pacific and 28 Atlantic specimens) Numbers given are those for Indo-Pacific specimens, those in brackets are for Atlantic specimens. The latter are given separately only if they differ from the former. D 13-15 [14-15], the first two unbranched; A 13-15 [13-14]; P 20-24 [20-23]; vertebrae (2 Pacific, 1 Atlantic specimens) 12 + 9 = 21. Head width 0.26-0.46 ($\bar{x}$ = 0.36; SD = 0.04) [0.33-0.43 ($\bar{x}$ = 0.38; SD = 0.03)], body width 0.33-0.51 ($\bar{x}$ = 0.42; SD = 0.05) [0.38-0.48 ($\bar{x}$ = 0.45; SD = 0.03)], peduncle length 0.09-0.20 ($\bar{x}$ = 0.15; SD = 0.03) [0.12-0.17 ($\bar{x}$ = 0.14; SD = 0.02)], eye 0.07-0.17 ($\bar{x}$ = 0.11; SD = 0.02) [0.08-0.15 ($\bar{x}$ = 0.12; SD = 0.02)]. Dorsal, anal, and caudal fins rounded, middle rays longest. Nasal tentacles with a pair of lateral openings.

S-D spines 12-16 [13-15], S-A spines 12-15, about 11 spine rows over the dorsum between pectoral fin bases, about 24 spine rows over the ventrum between pectoral fin bases. Four or five frontal spines. Longest frontal spine 0.13-0.28 ($\bar{x}$ = 0.18; SD = 0.03) [0.13-0.17 ($\bar{x}$ = 0.146; SD = 0.012)], pectoral axil spines 0.11-0.22 ($\bar{x}$ = 0.16; SD = 0.03) [0.11-0.17 ($\bar{x}$ = 0.144; SD = 0.013)]. Frontal spines generally longest on the body. Pectoral axil spines 0.89-1.38 ($\bar{x}$ = 1.12; SD = 0.11) [0.90-1.23 ($\bar{x}$ = 1.00; SD = 0.07)] in frontal spines. Dorsal, dorsolateral, and lateral spines about equal in length (ca. 1.1 in frontal spines). Ventral spines somewhat reduced (ca. 1.5 in frontal spines). Spines at base of dorsal fin moderate (ca. 1.5 in frontal spines) and extend over the peduncle, but no spines wholly on the peduncle. The subdermal lateral bases moderate (1.4-2.3 in shaft length) except in ventral spines where they may equal the shaft length. Shaft extension short, but present on all spines except those on the top of the head. No spines markedly reduced. A short, fixed tribase spine immediately above the gill opening and usually a second slightly posterior to it above the pectoral base. Three or four flat spines with broad lateral bases forming the anterior border of the gill opening. All but one of 86 Indo-Pacific specimens examined without a short, downward-pointing spine below the anterior border of the eye. However, Atlantic specimens usually have this spine on at least one side (52 of 58 examined).

Two small barbels on the chin. Specimens taken pelagically (5-86 mm) lack these as well as the fleshy tentacles described next. A set of fleshy tentacles is variably present; absence may be due to damage or poor preservation. The full set of tentacles consists of the following: 1) one over each eye, 2) one pair middorsally (ca. one-third of the way between pectoral fin base and dorsal fin), 3) two along each postpectoral dorsolateral edge, 4) two along each postpectoral ventrolateral edge, and 5) four along ventrolateral edge of head.

Background color in preserved specimens light tan or grey to medium brown. The color pattern dominated by several large dark brown to black blotches on dorsal and lateral surfaces. Blotches usually lack a distinct light colored border. Blotches arranged as follows (Figure 18): 1) one

round blotch around the base of the dorsal fin, 2) one middorsal blotch of variable shape about midway between the dorsal fin and pectoral base, 3) a round to squarish blotch above each pectoral fin along the dorsolateral surface just posterior to the fin base, 4) a broad transverse bar across the occipital region, 5) a bar beginning below each eye and extending on to the interorbital (in Indo-Pacific specimens this bar is usually continuous across the interorbital, but in Atlantic specimens it is often not), 6) occasionally, a rather diffuse lateral bar between eye and gill opening. The dorsal and lateral surface with scattered small (<pupil diameter) spots the same color as the blotches; these are variable in number and size and rarely may be entirely lacking; they are not associated with the spine axils. Ventral surfaces white, but may be marked with spots which tend to be larger than the dorsal spots. This "pelagic spotting" (Figure 19) of the belly (see section on Eggs, larvae, and pelagic stages) is always found on specimens taken pelagically, but is often retained on specimens collected inshore (60-200 mm); this seems to be the case particularly with eastern Pacific specimens. Pelagic spotting may extend dorsally to the level of the pectoral fin. No dark band on the underside of the head. Fins unspotted, except for some small clusters of melanophores associated with the fin rays. Color in life essentially the same as above, but fins may be yellowish and there may be yellowish areas around the spine bases.

The largest specimen examined was 289 mm. There are literature reports of much larger specimens, but these may be based on misidentifications. However, it is clear that *D. holocanthus* does not reach the size of *D. hystrix*.

Eggs, larvae, and pelagic stages.—The eggs and larvae of *D. holocanthus* were initially identified by rearing eggs from plankton tows. Three larvae were successfully reared through metamorphosis. These fish lived 25-33 days after hatching before being preserved. One was cleared and stained.

The eggs of *D. holocanthus* are spherical, with 10-30 clear, yellowish oil droplets of 0.05-0.25 mm in diameter. The eggs are pelagic, with a narrow perivitelline space, unsegmented yolk, and a

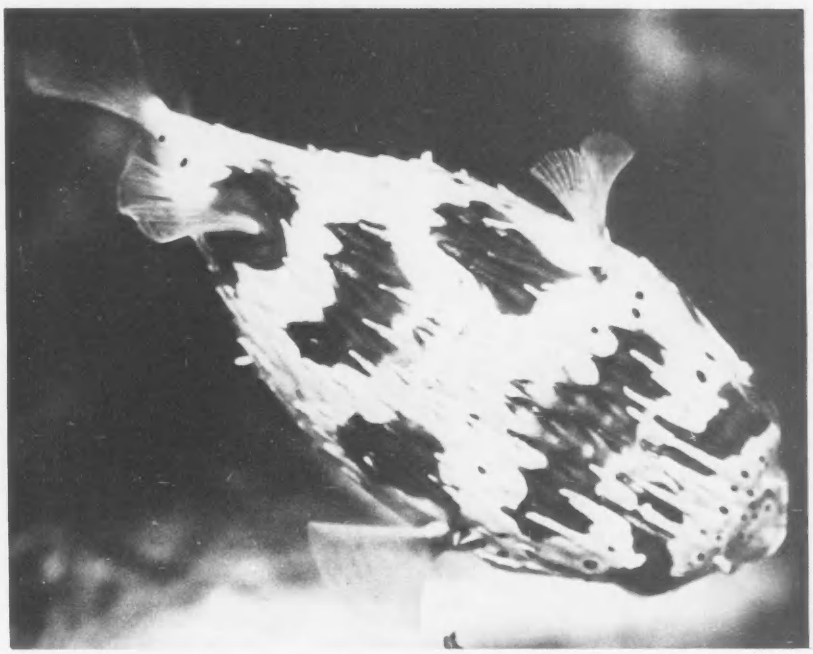

FIGURE 18.—Dorsal view of *Diodon holocanthus*, note interorbital bar. Oahu, Hawaiian Islands, 150 mm SL (HIMB, uncataloged).

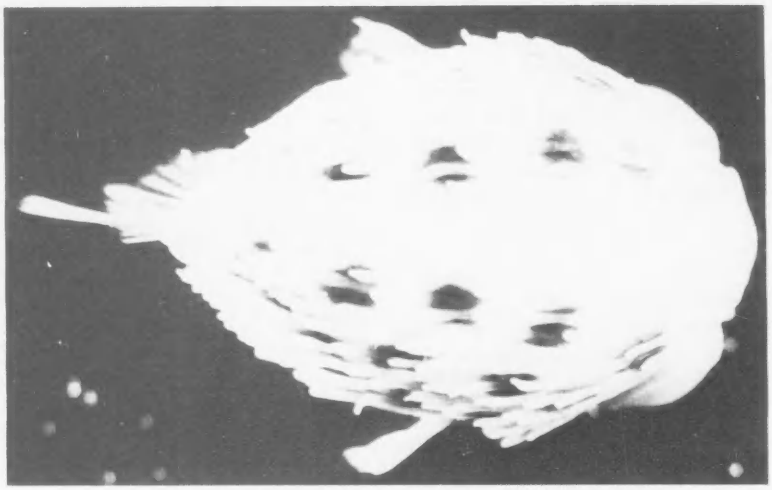

FIGURE 19.—Ventral view of pelagic juvenile of *Diodon holocanthus*, 14.5 mm SL, Hawaiian waters (HIMB, uncataloged). Note pelagic spotting.

clear, unornamented chorion. The diameter of the live eggs is 1.7-1.8 mm ($\bar{x}$ = 1.74; SD = 0.03; n = 16) and of preserved eggs is 1.6-1.8 mm ($\bar{x}$ = 1.69; SD = 0.06; n = 191). These means are significantly different at the 5% level (t-test) and a shrinkage of about 4% upon preservation in 5-10% seawater-Formalin[3] is indicated. Rearing experiments indicate that the eggs are spawned in the early evening and hatch in 4-5 days at about 25°C. In rearing containers, the eggs sink to the bottom 12-24 h before hatching.

Embryonic Development: The development of *D. holocanthus* eggs is similar to that of *Ranzania laevis* (see Leis 1977). Development is described here with emphasis on differences between these two species.

Early stage (preclosure of blastopore, Figure 20). The earliest eggs collected were in midgastrulation. The oil droplets are tightly clustered opposite the embryonic axis. These move with the germ ring to the caudal end of the embryo by blastopore closure where they subsequently start to disperse. The elapsed time between midgastrulation and blastopore closure is 3 h. Some segmentation can be perceived on the embryo, but in general little structure is evident. No pigment has formed.

Middle stage (blastopore closure to separation of the tail bud from the yolk, Figure 21). The oil droplets remain scattered over the caudal one-fourth of the yolk sac. The eyes, heart, brain lobes, and otic vesicles are formed within 18 h of blastopore closure. The head is broad and no pigment is visible.

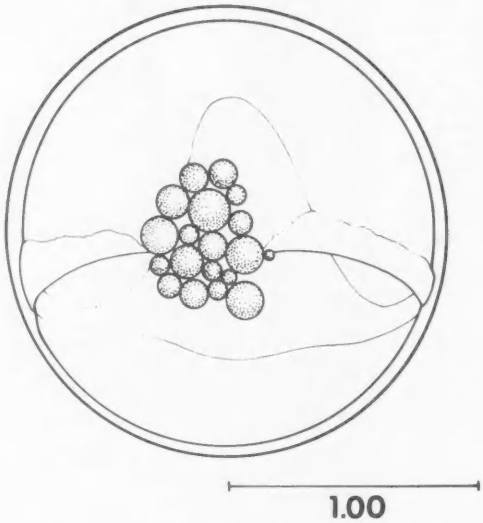

FIGURE 20.—Early stage egg of *Diodon holocanthus*. After Watson and Leis (1974), scale in millimeters.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

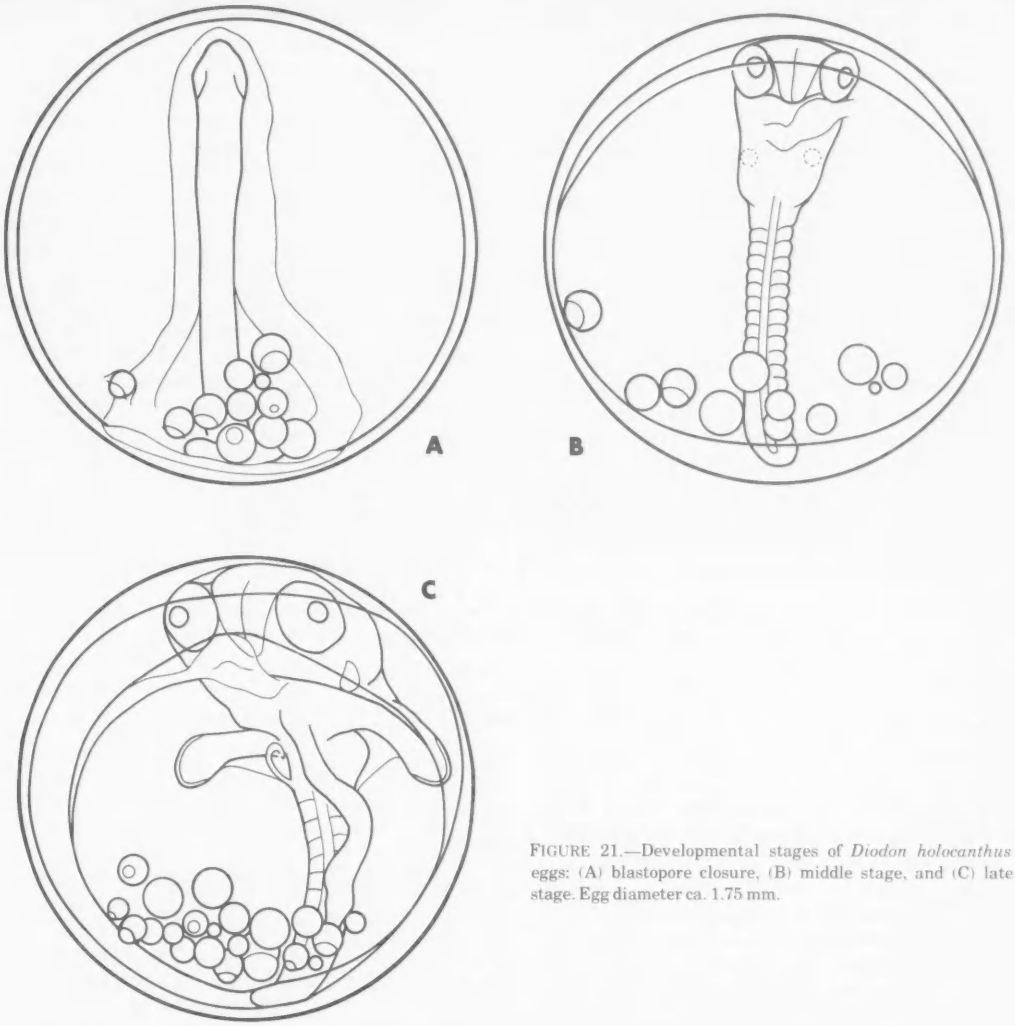

FIGURE 21.—Developmental stages of *Diodon holocanthus* eggs: (A) blastopore closure, (B) middle stage, and (C) late stage. Egg diameter ca. 1.75 mm.

Late stage (tail bud completion to first eye pigmentation and melanophores on body, Figure 21). The oil droplets are on the ventral surface of the yolk sac. The head becomes very broad and enclosed by an inflated vesicular dermal sac which eventually expands to enclose the entire body by the end of this stage. The pectoral fins are well-formed and are occasionally moved by the embryo. An odd hooklike structure which seems to be the incipient pectoral girdle can be seen in live material in the vicinity of the base. The gut forms a long, straight tube. The eyes develop their first pigment during this stage, and a few melanophores appear on the head and dorsal surfaces. At about this time red chromatophores appear, scattered throughout the dermal sac and on the fin buds and folds.

Final stage (acquisition of full eye pigmentation through hatching). The oil droplets are no longer visible, being enclosed with the yolk sac within the abdomen. The mouth apparently becomes functional now, and the exhalant gill openings are visible. The eyes are completely, if lightly, pigmented. Body melanophores have spread over most of the

dorsal surfaces. No melanophores are present on the postanal myomeres or on the dermal sac.

Identification of Eggs: The combination of size (>1.5 mm) and numerous oil droplets serves to distinguish the eggs of *D. holocanthus* from those of all other pelagic eggs except those of other tetraodontiform species. The eggs of the molid *Ranzania laevis* have been described by Leis (1977). *Ranzania laevis* eggs may be distinguished from *D. holocanthus* eggs by the former's smaller size (1.4-1.65 mm) and by the extensive pigment which develops on the ventral surface of the yolk sac of *R. laevis* in the middle stage.

Hawaiian ostraciid eggs (*Ostracion* and *Lactoria*) may be distinguished by their slightly oblong shape, fewer oil droplets (<10), but most reliably by a patch of bumps on the chorion surrounding the micropyle. This "rough patch" is easily overlooked.

Diodon hystrix eggs are the only other *Diodon* eggs known (see section on *D. hystrix*). They can be distinguished from those of *D. holocanthus* by their larger size (>1.9 mm), greater number of oil droplets (>30), and the orange (rather than red) pigment.

Larval Development: Fifteen reared and 12 field-collected larvae in good enough condition for descriptive purposes were available. Morphometric data are summarized in Table 4.

The newly hatched larva has well-developed, apparently functional eyes, jaws, and gas bladder (Figure 22). The pectoral fins are quite large, although no rays are formed. The larvae are 1.9-2.1 mm SL at hatching and the body is rotund. Development in reared larvae is slow. Dorsal and anal fin anlagen form by day 10 (2.4 mm, Figure 22); the olfactory pit also forms by this time and the eyes have become proportionally larger. The oldest reared larva available was 16 days old, but it was smaller than the

TABLE 4.—Morphometric and meristic data for larval and juvenile *Diodon holocanthus* (measurements in mm). ? indicates individuals of unknown age, from plankton samples; × indicates damaged.

Age (days) of reared fish	Notochord or standard length	Snout to anus length	Width of eye	Head length	Head width	Mouth width	Fin ray counts		
							D	A	P
Larvae:									
1	2.0	1.5	0.3	0.9	1.1	0.5	0	0	0
1	2.1	1.5	0.3	0.8	1.2	0.5	0	0	0
1	2.0	1.5	0.3	0.8	1.2	0.4	0	0	0
1	2.0	1.4	0.3	0.8	1.2	0.4	0	0	0
1	1.9	1.4	0.3	0.7	1.2	0.5	0	0	0
?	1.9	1.5	0.3	0.8	1.1	0.6	0	0	0
?	1.9	1.4	0.3	0.9	—	0.4	0	0	0
?	1.9	1.6	0.4	0.9	1.2	0.6	0	0	0
?	1.9	1.0	0.3	0.6	—	—	0	0	0
?	2.0	1.6	0.4	0.8	1.1	0.6	0	0	0
?	2.0	1.6	0.3	0.7	1.1	0.3	0	0	0
5	1.8	1.4	0.3	0.8	1.2	0.6	0	0	0
6	1.8	1.4	0.4	0.8	1.0	0.6	0	0	0
7	1.9	1.4	0.3	0.8	1.0	0.5	0	0	0
8	2.1	1.4	0.4	0.9	1.1	0.6	0	0	0
8	2.2	1.7	0.5	0.9	1.4	0.7	0	0	0
8	2.1	1.5	0.4	0.8	1.1	0.6	0	0	0
9	2.0	1.4	0.4	0.8	1.0	0.5	0	0	0
?	2.2	1.5	0.3	0.8	1.2	0.5	0	0	0
?	2.3	2.0	0.5	0.8	1.5	0.6	0	0	0
?	2.3	1.5	0.3	0.8	1.1	0.5	0	0	0
10	2.4	2.0	0.5	0.9	1.5	0.8	0	0	0
10	2.2	1.7	0.5	0.9	1.3	0.6	0	0	0
?	2.5	2.1	0.5	0.7	—	0.4	0	0	0
?	2.6	2.0	0.5	0.7	0.8	0.4	0	0	0
?	2.7	2.2	0.5	0.7	—	—	0	0	0
16	[1]1.9	1.5	0.5	1.0	1.2	0.7	0	0	0
Juveniles:									
?	3.8	3.4	0.8	1.9	2.6	1.0	×	×	22
25	4.8	4.0	1.0	2.3	3.5	1.9	14	14	23
?	5.5	4.8	1.1	2.8	3.3	1.6	—	—	—
?	6.0	5.3	1.2	3.3	3.5	1.8	—	—	—
33	6.7	5.2	1.4	2.9	4.3	1.7	15	×	21
?	7.2	5.5	1.5	3.4	3.7	1.7	14	14	23
ca. 30	8.1	6.7	1.8	3.9	4.8	1.8	14	14	21
?	11.0	9.0	2.0	5.5	6.3	2.7	—	—	—
?	14.1	10.9	2.7	6.3	7.6	3.2	15	14	23

[1]Fish in emaciated condition.

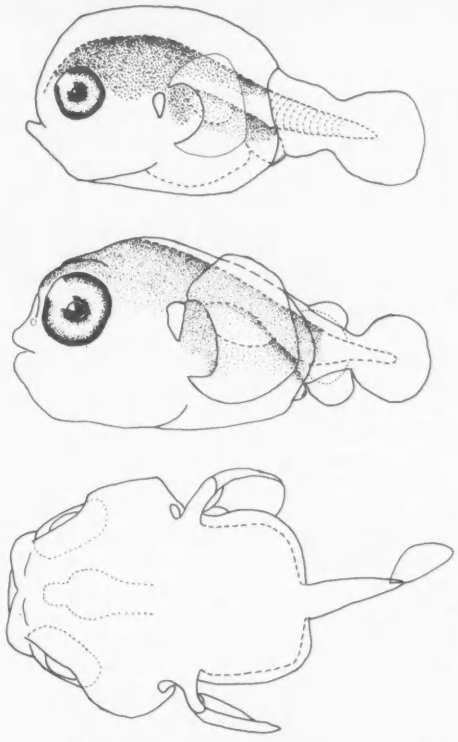

FIGURE 22.—Reared larvae of *Diodon holocanthus*: (top) newly hatched larva 2.0 mm, (middle) 10-day-old larva 2.4 mm, and (bottom) dorsal view of 10-day-old larva with pigment omitted.

day-10 larvae and appeared emaciated. There are incipient fin rays and bases visible in the fins of the 16-day-old larva, but it otherwise is not obviously advanced over the 10-day-old specimen. There is no sign of development of the caudal fin complex. The largest larva available is a 2.7-mm field-collected specimen which is no more advanced than the day-16 larva. The dermal sac is inflated in young larvae (Figure 22), but the subdermal space is virtually gone by day 10 (Figure 22).

The larvae are more or less uniformly pigmented with scattered melanophores on the dorsal surfaces at all stages. The pigment spreads laterally, but there is little below the level of the pectoral fin and the ventral surfaces remain devoid of melanophores until metamorphosis. The newly hatched larvae have no melanophores posterior to the anus (Figure 22), but by day 10 postanal pigment has spread to the middle of the dorsal fin anlage. In life, the newly hatched larva is covered with widely scattered red chromatophores on the dermal sac and fins. The red pigment persists through the larval stage and on about day 2 it is supplemented by a yellow background pigment covering all the body surfaces (not the dermal sac), but being most obvious ventrally due to a lack of melanophores there.

A 2.0-mm field-collected specimen was cleared and stained. The only ossified structures were the cleithrum, coracoid, and six branchiostegals.

Juvenile Development: Metamorphosis apparently occurs at ca. 3 mm at an age of about 3 wk. The smallest juvenile available is 3.8 mm and resembles Mito's (1966) illustration of a 3.7-mm juvenile except that Mito's fish had smaller eyes. The caudal, dorsal, anal, and pectoral fins are all formed as are the teeth, and the body is covered with small spines. The spines do not appear to be erectile, but the fish is capable of inflation. The spines are covered with a sheathlike tissue. They elongate rapidly with growth and by 4.8 mm SL (Figure 23) they are obviously erectile. The nostrils are formed in the 3.8-mm fish, although the nasal tentacle with two lateral openings is not formed until 4.8 mm SL, and in fish as large as 6.0 mm, it may be open at the ends. The 4.8-mm fish is in all respects a miniature adult with all external structures formed and functional. External changes to the adult stage involve only changes in proportion; the spines in particular elongate, the body becomes less rotund and the eye relatively smaller. Morphometric and meristic data are summarized in Table 3.

A 33-day-old juvenile of 6.7 mm was cleared and stained. The vertebral column and skull are incompletely ossified but all other structures are ossified. The vertebral formula is $12 + 9 = 21$ and the vertebral column is strongly arched. There are 11 dorsal and 11 anal pterygiophores which are associated with vertebrae 12-16 and 13-17, respectively.

At metamorphosis, pigment changes radically. The background color in live material is still predominantly yellow with scattered red chromatophores but this does not persist. Dorsally, the melanophores are scattered fairly uniformly, with a concentration at the pectoral base and very little pigment on the caudal peduncle.

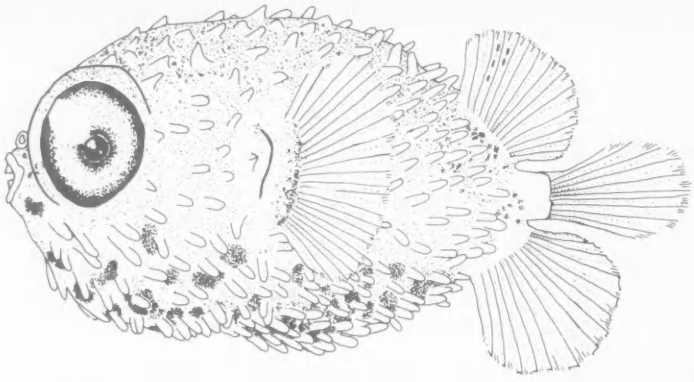

FIGURE 23.—Reared juvenile of *Diodon holocanthus*, 4.8 mm SL, 25 days old. Note pelagic spotting. Hawaiian material.

Ventrally, however, a number of distinct spots have formed that cover the belly (Figure 23). The spots (pelagic spotting) are at first close together but become less numerous and proportionately larger, aligning in rows with growth (Figure 19). Dorsal spotting (always more diffuse than ventral spotting) begins to form at around 10 mm and the characteristic dorsal blotch pattern is generally visible by 30 mm, although in pelagic specimens the contrast with the background color is not great. The pelagic spotting is retained in all pelagic individuals examined (to 86 mm) and in some specimens collected inshore. The fins remain unpigmented except for a few melanophores along the fin rays of the dorsal fin.

Identification of Larvae and Juveniles: Diodontid larvae are likely to be confused only with the rotund, heavily pigmented, sac enclosed ceratioid larvae and other tetraodontiform larvae. Reference to Bertelsen's (1951) work should allow ceratioid larvae to be distinguished as such. Rotund tetraodontiform larvae may be distinguished from diodontid larvae as follows: molids by their body spination and early forming pectoral rays; ostraciids by their pigmentation and early forming pectoral rays; tetraodontids by their relatively more elongate body shape and early forming fin rays. *Diodon* larvae are heavily pigmented only on dorsal surfaces, do not develop fin rays until near or at metamorphosis, have very wide heads and bodies (>body depth), and have very wide mouths.

The larvae of *D. holocanthus* can be distinguished from the putative *D. hystrix* larvae, the only other larval diodontid known, by the less well-developed condition at hatching of the latter (see section on *D. hystrix*). In addition, *D. hystrix* larvae are predominantly orange upon hatching while those of *D. holocanthus* are yellow. Melanophores of *D. holocanthus* do not extend onto the postanal myomeres past the middle of the dorsal and anal fin anlagen; the postanal myomeres of *D. hystrix* are moderately pigmented. Lastly, the eyes of *D. hystrix* larvae are smaller than those of *D. holocanthus* larvae (Tables 2,3).

Once the spines form, the lack of caudal peduncle spination, fin ray counts and spine placement serve to distinguish *D. holocanthus* from all other *Diodon* species (see Key).

The duration of the pelagic stage is unknown, but judging from reared specimens, metamorphosis occurs about 3 wk after hatching at about 4 mm SL. The largest individual captured pelagically was 86 mm while the smallest captured inshore was 60 mm. A certain amount of plasticity in the duration of the pelagic stage is indicated, but its length clearly must be measured in terms of months. No special adaptations for pelagic life are evident in these juvenile stages except, perhaps, in color. In the tetraodontiform fishes (except the molids) the larval stage is short and relatively unspecialized, while a relatively unmodified pelagic juvenile stage may be quite long (see Remarks under *D. eydouxii*). This strategy (for dispersal?) is in marked contrast to that in many advanced perciform shorefishes (e.g., Acanthuridae, Chaetodontidae) where bizarrely modified and long-lived larval and pelagic prejuvenile stages are developed which subsequently undergo marked (and rapid) metamorphosis upon becoming benthic.

Diodon holocanthus eggs and larvae have been found in Hawaiian waters from February through September, with an apparent peak in abundance in May-June, although they are never common. Larvae usually occurred singly in plankton tows (volume filtered 200-1,000 m^3). Although as many as 30 eggs/1,000 m^3 have been taken, 1-5 eggs/1,000 m^3 were more usual, and most tows contained none. Eggs were usually found close to shore, but larvae rarely were found closer than 1 km from shore (pers. observ.).

Holotype.—No holotype or type-series is known to exist. Linnaeus based his description on that of Artedi (1738).

Distribution.—*Diodon holocanthus* is circumtropical in distribution, but is seemingly absent in the southwest and central Pacific east of the andesite line (the separation of continental from oceanic rocks, Figure 14). However, it reappears in Hawaii, Pitcairn, and Easter Islands. Cuvier's holotype of *D. quadrimaculatus* was allegedly collected by Peron in Tahiti (see Le Danois 1961). Inasmuch as it is known that much of the locality data accompanying Peron's specimens are incorrect (associated with a shipwreck, see Whitley 1931:25) this record is questionable. There is evidence of divergence of the Atlantic population(s) from those of the Indo-Pacific (see Remarks).

Remarks.—I follow the spelling *holocanthus* (rather than *holacanthus* of many authors) which was used consistently by both Linnaeus and Artedi (see also Bailey et al. 1970), and is thus not considered to be a misprint as maintained by Jordan and Evermann (1891). Linnaeus' description is brief; the only useful information being the statement that the spines are terete and extremely long on the head and nape. However, this can apply only to *D. nicthemerus* or *D. holocanthus*. Assuming that "Habitat in India" means India as understood today, and not the entire Indo-Pacific, *D. nicthemerus* is eliminated. However, even if "Habitat in India" means the entire Indo-Pacific, it is unlikely that specimens of *D. nicthemerus*, a species apparently confined to southern Australia, could have reached Artedi by 1738. In any case, subsequent usage and stability demand that the name *D. holocanthus* apply to the species described above.

Diodon pilosus is synonymized with *D. holocanthus* on the basis of Mitchill's observation that no spines were present between the dorsal and caudal fins of his small (ca. 38 mm) New York specimen. *Diodon holocanthus* is the only Atlantic species that lacks peduncle spines. Mitchill distinguished *D. pilosus* on the basis of its flxible spines, but this is the usual condition in small specimens. No holotype is known to exist.

Cuvier's types are extant. Information and photographs of these specimens (catalog numbers and other information are given by Le Danois 1961) provided by M. L. Bauchot (pers. commun., MNHN, 20 May 1975) clearly establish *D. novemmaculatus*, *sexmaculatus*, *quadrimaculatus*, and *multimaculatus* (all of Cuvier) as junior synonyms of *D. holocanthus*. Inasmuch as Cuvier's (1818) descriptions are relatively clear, only his *D. novemmaculatus* requires comment. The holotype of *D. novemmaculatus* (MNHN A.9928, 107 mm) is *D. holocanthus*, apparently from the Atlantic (no locality data are available for this specimen). A spine is present below the anterior margin of the eye and the eye bar is discontinuous over the interorbital. Unfortunately, Cuvier's figure resembles *D. liturosus* as much as *D. holocanthus* (the figure shows the frontal spines shorter than they actually are). This probably led Bleeker (1865) to apply the name *D. novemmaculatus* to *D. liturosus*.

Diodon maculifer Kaup (1855) is included here with some questions. Kaup's description is of little help, and no type material can be found in the British Museum where it would be expected to reside. The holotype may have been part of Kaup's lost personal collection (A. C. Wheeler, pers. commun.). Examination of one of the South African (Kaup's type-locality) specimens of "*Diodon maculifer*" listed by Günther (1870) (BMNH 1845.7.3.103, 100 mm, loaned by A. C. Wheeler) reveals it to be an inflated, dried *D. holocanthus*. In this specimen, inflation is so great (an artifact of stuffing and drying?) that the subdermal spine bases project through the dried skin. Thus, the base of the spines appear to be expanded and transversely compressed. The only characteristic feature of Kaup's description is the compressed nature of the spines, and it seems likely that his description was based on a dried, inflated *D. holocanthus*.

Steindachner's *Atopomycterus bocagei* can be placed in the synonomy of *D. holocanthus* on the basis of information on the holotype (NMV 63848)

provided by P. Kähsbauer (pers. commun., NMV, 1975). Steindachner's (1866) description is essentially correct and unquestionably refers to *D. holocanthus*. The placement of this specimen in *Atopomycterus* was apparently based on the split nasal tentacle (see section on *D. nicthemerus*). A single split nasal tentacle was present on only 3 of the more than 100 specimens of *D. holocanthus* examined, so this condition is rare but not unprecedented.

Both *D. liturosus* Shaw and *D. maculatus* Lacepède (the Latinized version of Le Diodon Tacheté) have been incorrectly applied to *D. holocanthus* by various authors (see section on *D. liturosus*).

For about the past 50 yr the chief sources of confusion on the identity of *D. holocanthus* have been confusion with *D. histrix* by some (mostly American) authors and the lumping of *D. liturosus* under *D. holocanthus* by nearly all authors. The latter problem is discussed under *D. liturosus*.

The confusion between *D. hystrix* and *D. holocanthus* stems primarily from three sources. Many authors (e.g., Gosline and Brock 1960) have conjectured that *D. holocanthus* is the young of *D. hystrix* because the former does not reach a large size, and few, if any, small specimens of the latter were available. However, as discussed under *D. hystrix*, this species is pelagic to ca. 200 mm and is thus unavailable to inshore collecting. Inasmuch as *D. holocanthus* does not commonly exceed 200 mm, the confusion was perhaps understandable.

Second, many early descriptions are poor and keys often rely solely on the size of frontal spines relative to the pectoral axil spines to distinguish the two species. Especially in Atlantic specimens of *D. holocanthus*, the frontal spines are likely to be approximately the same size or even shorter than the pectoral axil spines.

Finally, as noted by Clark and Gohar (1953) (see also Bagnis et al. 1972:225), living *D. hystrix* often display a dorsal blotch pattern not unlike that of *D. holocanthus*. I have not observed this color pattern in preserved *D. hystrix*.

The apparent divergence of the Atlantic and Indo-Pacific populations of *D. holocanthus* mentioned above is of interest. At present, since *D. holocanthus* is apparently absent from the Red Sea and the Mediterranean, gene flow could occur only around southern Africa. Evidence that this is apparently not happening comes from the Indian Ocean specimens which lack a snout spine and have very long frontal spines in contrast to the Atlantic specimens (Table 5). In addition, Poll's (1959) description (as *D. hystrix*) of a west African specimen is typical of the specimens from the western Atlantic examined by me. The apparent increase in frontal spine length from the Atlantic to the Pacific to the Indian Oceans is curious. Based on studies of other groups (Ekman 1967) affinities might be expected between the Atlantic and eastern Pacific populations, but no extension to Hawaii and Easter and Pitcairn Islands would be expected. The lack of the snout spine in all but the Atlantic population and one Hawaiian specimen may indicate that the Atlantic population is distinct. Fin ray counts are of little help in resolving this question. Because all the characters which appear to differ between the Atlantic specimens and those from other areas are rather variable (although some are significantly different in a statistical sense), I choose not to distinguish formally the populations nomenclaturally at the subspecific level. If future study shows this split to be desirable, the proper name for the Atlantic specimens would be *Diodon holocanthus pilosus* Mitchill.

Le Danois (1954) reported sexual dimorphism in *D. holocanthus*, but her illustration of a female *D. holocanthus* (p. 2355:fig. 3) appears to be *D. liturosus*.

Material examined.—141 specimens, 5-289 mm.

EASTERN PACIFIC: NMFS LJ (1:18.5) 18°56′N, 104°10′W; NMFS LJ D31-133.25 (1:64.5) 26°04.5′N, 112°48.0′W; NMFS LJ TO-5801 (1:85.5) 5°29.5′N, 77°57′W; NMFS LJ (1:73.5) "350 mi. west of Costa Rica"; NMFS LJ B-5011 157.40 (2:41-41.5) 21°32.5′N, 111°14.5′W; UA 66-39-18 (1:242) San Agustin Bay, Sonora, Mexico; UA 69-35-25 (1:245) Guaymas, Sonora, Mexico;

TABLE 5.—Comparison of selected characters of *Diodon holocanthus* from five regions (see also Figure 6). n = number of individuals examined for snout spine.

Area	n	No. with snout spine	Frontal spine/SL	Fin rays ($\bar{x}$) D	Fin rays ($\bar{x}$) P	Interorbital bar
Atlantic	58	52	0.146	14.15	22.15	Usually discontinuous
E. Pacific	11	0	0.154	13.80	22.10	Usually continuous
Hawaii, Pitcairn, and Easter Is.	24	1	0.174	14.44	22.57	Usually continuous
W. Pacific	29	0	0.205	14.11	22.17	Usually continuous
Indian	6	0	0.200	13.80	21.92	Usually continuous

UA 71-63-8 (1:145) Puerto Vallarta, Jalisco, Mexico; UA 71-65-9 (1:126) Isla Jaltemba, Jalisco, Mexico; SIO 59-373 (1:ca. 200) La Jolla, Calif.; SIO 63-82 (1:ca. 90) Cape Marco, Columbia. HAWAIIAN IS.: HIMB (3:135-289), HIMB 67-58 (1:67) Kaneohe Bay, Oahu; HIMB (1:181) Punaluu, Oahu; BPBM 10635 (1:63), BPBM 6977 (1:167) Diamond Head, Oahu; BPBM 5124 (1:129) French Frigate Shoals; NMFS H TC32-6,9,11,14 (6:12.5-30) 21°22′N, 158°14′W; NMFS H TC32-23 (1:14) 21°00′N, 158°30′W; NMFS H TC32-73 (1:7.0) 19°31′N, 156°06′W. SOUTHEAST PACIFIC: (all BPBM) 16459 (2:144-168), 13251 (1:135), 16455 (1:122) Pitcairn I.; 6797 (1:150.5), 6798 (1:185), 6799 (1:158), 6800 (1:156.5) Easter I. WESTERN PACIFIC: GVF stn HK91 (2:85-109) 19°38′N, 111°30′E; GVF 2269 (1:128) Gulf of Thailand; CAS 29126 (1:32) Ternate, Moluccas; CAS 6987 (1:41) Misaki, Japan; CAS 6752 (3:100-114) Wakanoura Kii, Japan; CAS 53402 (1:225) Hachijo I., Japan; CAS 15849 (10:90-125) Taiwan Strait. AUSTRALIA: AMS I.17228-001 (10:67-91) New South Wales. INDIAN OCEAN: RUSI 2782 (1:47.5) Knysna, South Africa; RUSI 3709 (1:60.5) East Cape, South Africa; RUSI 3710 (1:65) Inhaca, Mozambique; BPBM 19022 (2:173-188) Negombo, Ceylon; BPBM 20255 (1:195) Wolmar, Mauritius. WESTERN ATLANTIC OCEAN: CAS 4761 (1:150) Jamaica; CAS 54039 (1:94) Havana, Cuba; CAS 18182 (2:50.5-57.5) 29°14′N, 88°19′W; CAS 17184 (1:91) Pine I., Fla.; GCRL VTS:11184 (1:113) San Blas, Panama; LACM 1463 (1:84.5) Key Biscayne, Fla.; LACM 6281, 6282, 6283, 6284, 5781, 5872 (23:64-159) southern Jamaica; NMFS LJ *Gill* 3-64 (1:59) 33°29′N, 76°40′W; NMFS LJ *Silver Bay* 3458 (1:60) 29°03′N, 78°04′W; NMFS M *Oregon II*-72-39-144 (1:12.5) 23°34′N, 82°22′W, 39-73 (1:13) 21°31′N, 86°14′W, 39-50 (1:24) 16°50′N, 80°13′W, 39-48 (1:24.5) 17°26′N, 79°26′W, 39-58 (1:30) 21°01′N, 80°14′W, 39-63 (2:10-40) 19°41′N, 84°13′W, 39-01 (1:23) 13°00′N, 60°00′W, 39-39 (1:45) 18°00′N, 73°00′W, 39-11 (1:56.5) 17°25′N, 63°00′W; NMFS M *Bowers* 75-126-8 (1:28) 26°00′N, 79°30′W; NMFS M *Oregon II*-76-66-19786 (2:23-32) 18°18′N, 75°22′W, 66-19789 (2:20-30) 18°49′N, 74°44′W, 66-19790 (6:27-34) 19°22′N, 75°44′W, 66-19791 (18:19-33) 17°50′N, 74°47′W.

Note.—Since this paper was accepted for publication, NMFS H and most HIMB specimens were transferrred to BPBM.

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PROBABLE CASE OF STREAMBED OVERSEEDING—1967 PINK SALMON, *ONCORHYNCHUS GORBUSCHA*, SPAWNERS AND SURVIVAL OF THEIR PROGENY IN SASHIN CREEK, SOUTHEASTERN ALASKA

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ABSTRACT

The 1967 escapement of 38,067 pink salmon, *Oncorhynchus gorbuscha*, to Sashin Creek, southeastern Alaska, was the largest since 1942. Studies on distribution and density of spawners and freshwater survival of their progeny indicated that deposition of excessive numbers of eggs caused a severe compensatory mortality of alevins during winter. Spawner density was 1.7, 1.6, and 1.2 females/m² in upper, middle, and lower study areas respectively. The greater density of spawners in the upper area in the odd-numbered years may be determined by genetic factors like timing of escapements and by greater marine survival of fry from the upper area. Based on the previously consistent relation between timing of adult entry and resulting freshwater survival, 1967 spawners should have produced 8 million fry rather than the 3 million that were produced.

Mortality of eggs and alevins was high during spawning, low between spawning and hatching, and high between hatching and emergence. Between 1 December 1967 and 25 March 1968, 11.1 million eggs or alevins, 10.7 million of which were alive on 1 December, disappeared within the streambed. Initial mortality of these progeny probably occurred in the early alevin stage from oxygen privation, whereas disappearance was probably related to rapid decomposition and invertebrate scavenging. A "snowball effect" is postulated whereby alevins that die shortly after hatching place increasing demands on available oxygen, causing accelerated mortality. A review of historical patterns of fry production in Sashin Creek indicates that streambed overseeding occurred in 1967.

Studies of pink salmon, *Oncorhynchus gorbuscha*, in Sashin Creek, Baranof Island, southeastern Alaska, have shown that certain factors markedly affect freshwater survival. These factors include: 1) seasonal timing of spawning (Skud 1958); 2) density and distribution of adults on the spawning grounds relative to ecological characteristics of the stream, especially gradient (Merrell 1962); and 3) quality of the intragravel environment, including oxygen content of intragravel water and amount of silt and fine particulate material in streambed gravels (McNeil 1966, 1968). Other factors of significance, but believed to be of less influence on freshwater survival in Sashin Creek, include predation on eggs and alevins (McLarney 1967), stream discharge during spawning (Ellis 1969), and incubation (McNeil 1968).

The spawning ground of Sashin Creek extends from the head of tidewater to an impassable falls 1,200 m upstream and includes 13,629 m² of streambed. Ninety-six percent (13,084 m²) of this ground comprises three distinct ecological areas that differ in gradient and size of particles in the substrate. McNeil (1966) called the areas upper, middle, and lower and described them briefly as follows: upper (2,945 m²)—relatively steep gradient (0.7%) and coarse streambed gravel; middle (4,067 m²)—intermediate gradient (0.3%) and medium-sized streambed gravel; and lower (6,072 m²)—low gradient (0.1%) and relatively fine streambed gravel. The remaining 4% (545 m²) of spawning ground is located in a short section of stream between the counting weir and the lower area and is not treated in this paper.

Pink salmon spawners entering Sashin Creek (the escapement) have been counted at a weir at the mouth of the creek since 1934, and the resulting numbers of fry from these escapements have been determined since 1940. During this time, the number of spawners varied from as few as 8 to more than 90,000 and the number of fry produced varied from 50 to almost 6 million. The percentage of freshwater survival, based on the estimated potential egg deposition, ranged from 0.06 to 21.75% (Table 1).

The high escapement of 38,067 pink salmon spawners in 1967, following a long series of relatively low escapements, gave me an opportunity to

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TABLE 1.—Number of adult pink salmon, potential egg deposition, number of fry produced, and freshwater survival in Sashin Creek, 1934-67. (Modified from McNeil 1968.)

Brood year	Number of adults	Potential egg deposition[1]	Number of fry produced	Percentage freshwater survival
1934	7,917	—	—	—
1935	6,323	—	—	—
1936	5,364	—	—	—
1937	9,085	—	—	—
1938	6,467	—	—	—
1939	16,830	—	—	—
1940	53,594	52,858,000	3,399,900	6.43
1941	84,303	88,678,000	1,024,300	1.16
1942	92,085	78,894,000	674,000	0.85
1943	14,883	14,980,000	227,800	1.52
1944	4,050	3,904,000	105,600	2.71
1945	5,465	5,062,000	43,100	0.85
1946	933	736,000	1,200	0.16
1947	1,486	1,330,000	27,600	2.07
1948	597	516,000	9,100	1.76
1949	4,902	4,800,000	176,200	3.67
1950	112	86,000	50	0.06
1951	4,366	4,062,000	412,500	10.15
1952[2]	45	—	740	—
1953	1,164	1,284,000	95,400	7.43
1954	21	12,000	660	5.48
1955	9,267	10,286,000	266,200	12.31
1956	933	1,018,000	5,040	0.50
1957	2,834	2,588,000	562,900	21.75
1958	217	174,000	10,700	6.13
1959	35,391	40,379,000	5,332,400	13.21
1960[2]	162	—	480	—
1961	28,759	29,425,000	5,940,300	20.19
1962[2]	8	8,000	100	1.20
1963	16,757	16,640,000	3,256,300	19.57
1964	[3]2,193	2,230,000	[4]310,000	13.91
1965	14,833	12,668,000	[4]2,235,000	17.92
1966	5,761	6,255,000	[4]744,000	11.99
1967	38,067	44,384,000	3,007,200	6.78

[1]Based on 2,000 eggs/female except when actual fecundity was calculated.
[2]An attempt was made to destroy the spawners or their progeny.
[3]Natural returning adults (327) were supplemented by the introduction of 1,866 adults taken from Bear Harbor, Kuiu Island.
[4]Fry weir not operated; figures are estimates of live alevins in the gravel just before start of emergence.

study the effects of a large spawning population on freshwater survival. For the 1967 escapement I studied 1) timing of entry into the stream and the distribution and density of pink salmon on the spawning grounds, and 2) survival of progeny by time periods in the three ecological areas of the stream and the overwinter disappearance of eggs and alevins from streambed gravels. In this paper I present all the available data on escapament size and production of fry in Sashin Creek and develop the hypothesis that streambed overseeding occurred in 1967. As Ricker (1962:186) pointed out, detailed knowledge on the effects of overseeding is important in understanding why pink salmon populations fluctuate. He stated, "Because it [overseeding] happens rarely nowadays, no chance should be lost to make such a study if one occurs." Simply stated, overseeding can be defined as an egg density in spawning bed gravels that leads to a significantly greater freshwater mortality than a lesser density would cause. As discussed more fully later, it is a complex and dynamic interaction between egg density, streambed ecology, and specific climatic conditions.

TIMING OF ENTRY AND DISTRIBUTION AND DENSITY OF SPAWNERS

The timing of stream entry was determined from daily counts of the adults at the Sashin Creek weir. This timing apparently influences the freshwater survival of the progeny. An inverse relation between time of stream entry of spawners and survival of progeny is usual in Sashin Creek (Skud 1958; Merrell 1962; McNeil 1968; Ellis 1969): high survival has been associated with early spawning and low survival with late spawning. Merrell (1962) further pointed out that pink salmon spawn in Sashin Creek an average of 12 days earlier during odd years than even years.[2] As a result, freshwater survival is usually higher among progeny of spawners from odd years than among those from even years (Table 1).

In 1967, 50% of the spawners had entered Sashin Creek by 20 August, the second earliest date on record. The early entry indicated that survival of eggs and alevins would be high, but this did not prove to be the case.

Throughout the run, random lots of females were tagged at the weir, and the distribution and density of spawners were determined from daily counts of both tagged and untagged females on the spawning grounds. This technique, described by McNeil (1968) and used by Ellis (1969), provides two methods of estimating the numbers of females spawning in the upper, middle, and lower areas. One method assumes that tagged females distribute themselves among the three sections the same as untagged females. In the other method, the summed daily count of all females in each area is divided by the average longevity on the spawning grounds. The results from the two methods were generally in agreement, except for the upper area where estimates based on distribution of tagged females were considerably higher than those based on total females. The difference may reflect the difficulty in making accurate counts on spawning riffles where densities of spawners are high; in such a situation an observer might count small

[2]The date when 50% of the escapement to Sashin Creek had entered the stream has been commonly used as an index of time of spawning.

numbers of tagged females more accurately than large numbers of untagged females. Because the relative accuracy of the two methods is unknown, I averaged them to arrive at mean estimates of densities of females in the three areas (Table 2).

Spawner density in Sashin Creek is usually unequal in the three study areas, depending in part on the total number of spawners. Densities in 1967 were the highest recorded for specific areas[3] of the stream (Table 3). Merrell (1962) noted that in years when many spawners were present, they utilized all of the available spawning grounds, and in years when few were present, they spawned mostly in the lower portion of the stream. When the upper area was used, survival of eggs and alevins in that area was higher and the number of fry produced was proportionally much greater than in the middle and lower areas (Merrell 1962). In addition, the sediment content and water quality of the stream in the upper area were better than in the other two areas (McNeil 1966, 1968). Sashin Creek thus presents an apparent paradox—the least favorable areas are used in years of relatively few spawners, and the best areas are used only during years of great numbers of spawners.

Merrell (1962) thought that the greater use of the upper area was related primarily to density-dependent spawner interactions. In 1967, however, the heavy use of the upper area was apparently not the result of high densities downstream forcing spawners into upstream areas: spawner densities in the upper area built up rapidly before spawning reached significant levels in the middle and lower areas. Although the upper area contains only 22% of the combined spawning grounds of the three areas, in 1967, 62% of the first group of female pink salmon tagged at the weir spawned in the upper area (Table 4). In general, the intensity of spawning in 1967 progressed to downstream areas from the upper area rather than the reverse. McNeil (1966, 1968) noted similar downstream shifts in spawning in Sashin Creek in 1963 and 1965. Although McNeil (1966) felt that the shift occurred because of heavy rainfall during the spawning period, he later noted (McNeil 1968) the same phenomenon during an unusually dry year.

It appears that the upper area in Sashin Creek is not necessarily used because of spawner overflow but because of more complex factors. Two interrelated factors could account for the spawner distributions observed in recent years: 1) migratory behavior associated with timing of the escapement, and 2) a genetic tendency for odd-year spawners to use upstream areas. Odd-year spawners enter the stream earlier than even-year spawners. A characteristic of early stream entry in anadromous fishes may be a tendency to migrate farther upstream than spawners associated with late stream entry (Briggs 1955). In addition to early entry and use of the upper area, odd-year spawners for the past 9 or 10 generations have consistently had higher escapements and, except for 1967, higher freshwater survival of progeny than even-year spawners (Table 1). Natural selection may be operating, in recent odd-year generations, to encourage progeny produced in the upper area to spawn in that area. Wells and McNeil (1970) showed that fry produced in the upper area of Sashin Creek were larger and presumably of better quality than those produced in the downstream areas. Differential marine survival

[3]Although the total number of spawners entering the stream has been recorded since 1934 (Table 1), detailed studies on the distribution of spawners in the upper, middle, and lower areas of the stream have been available only since 1961.

TABLE 2.—Estimated densities of female pink salmon spawning in three areas of Sashin Creek, 1967.

	Females per square meter		
Area	Based on counts of tagged females only	Based on counts of tagged and untagged females	Mean
Upper	1.90	1.59	1.74
Middle	1.49	1.76	1.62
Lower	1.19	1.15	1.17

TABLE 3.—Estimated densities of female pink salmon spawning in three areas of Sashin Creek, 1961-67.

	Females per square meter					
Area	1961[1]	1963[2]	1964[3]	1965[4]	1966[5]	1967
Upper	1.00	0.59	0.01	0.58	0.04	1.74
Middle	1.00	0.89	0.09	0.62	0.27	1.62
Lower	1.00	0.59	0.13	0.44	0.28	1.17

[1]Extrapolated from subjective estimate (McNeil et al. 1964).
[2]Adjusted from McNeil (1966).
[3]McNeil et al. (1969).
[4]McNeil (1968).
[5]Ellis (1969).

TABLE 4.—Dates of tagging and percentage of total escapement counted through weir, numbers of female pink salmon tagged, and spawning distribution of tagged females in three areas of Sashin Creek, 1967.

Date of tagging[1]	Percentage of total escapement counted through weir	Females tagged	Tagged females observed spawning	Percentage of tagged fish accounted for		
				Upper area	Middle area	Lower area
10 Aug.	3	49	40	62	25	12
12 Aug.	13	50	40	22	37	40
17 Aug.	26	50	42	21	23	55
20 Aug.	54	50	50	22	42	36
5 Sept.	98	50	40	22	30	48

[1]Females tagged on each date received color-coded tags that differentiated them from females tagged on other dates.

that favored fry produced in the upper area over those produced in the downstream areas could account for the greater escapements of odd-year spawners in recent years.

SURVIVAL OF EGGS AND ALEVINS

Survival of eggs and alevins from the 1967 brood year was estimated in Sashin Creek for four time periods: 1) from stream entry to end of spawning, 2) from end of spawning to hatching, 3) from hatching to shortly before fry emergence, and 4) from shortly before emergence to emergence and downstream migration of fry.

The estimates of survival were based on estimates of the potential egg deposition of female spawners and estimates of the surviving eggs and alevins in the three study areas. Potential egg deposition was estimated by multiplying the number of females by average fecundity. Densities of eggs and alevins were determined after spawning, during hatching, and before fry emergence by sampling randomly selected 0.1-m^2 points in the streambed with a hydraulic sampling technique described by McNeil (1964a). The number of fry migrating from the stream were estimated on the basis of daily counts of fry migrating through a weir at the stream mouth.

Numbers of females entering the stream and average fecundity were derived from counts and samples taken at the weir. Of the 38,067 pink salmon spawners entering Sashin Creek in 1967, 19,639 (52%) were females. Total counts of mature eggs from each of 35 females selected at random from the run ranged from 810 to 2,954 (average 2,260) eggs/female (90% confidence limit of mean fecundity was ±115 eggs).

The percentage of eggs available for deposition that are actually buried in the streambed is partly dependent on the density of spawners. McNeil (1964b) discussed the role of redd superimposition and showed that at spawner densities approaching 3 to 4 females/m^2 of spawning ground, an upper asymptotic limit on the density of eggs in the streambed is reached. Factors other than spawner density that may influence egg deposition include loss of adults in the stream before spawning and retention of eggs in the female's body (Neave 1953), type and characteristics of the spawning substrate (McNeil 1966), streamflow during spawning (Ellis 1969), and loss of eggs to vertebrate predators during the spawning process (Moyle 1966; McLarney 1967; Reed 1967).

The efficiency of egg deposition of pink salmon spawners in Sashin Creek is highly variable, from 37 to 82% of the potential egg deposition (Ellis 1969). In 1967 the number of pink salmon eggs potentially available for deposition was 44.4 million, with 19.9 million of these (45% of the potential) estimated to be in the streambed after spawning. The efficiency of egg deposition was 47% in the upper area, 50% in the middle area, and 38% in the lower area.

Although spawner densities were high in 1967 (Table 3), the ability of pink salmon to void most of their eggs during spawning did not seem to be affected. Egg retention is characteristically low in Sashin Creek, usually less than 5% of fecundity (McNeil 1966; Ellis 1969). In 1967, I examined the body cavities of 402 spent female pink salmon (about 2% of the total) and found that average egg retention was 1.5% of average fecundity.

The proportion of eggs actually deposited that were alive at the end of the spawning period in 1967 was highest (93%) in the upper area, intermediate (83%) in the middle area, and lowest (74%) in the lower area (Table 5). This high survival in the upper area is consistent with that of previous years. The ratio of live to combined live and dead eggs and alevins was usually higher in the upper and middle areas than in the lower area through hatching to the beginning of fry emergence (Table 5).

Survival of eggs and alevins varied among the three time periods (during spawning, between end of spawning and hatching, and between end of hatching and emergence). Survival within each time period for each area was higher between spawning and hatching than during spawning or between hatching and emergence (Table 6). As previously discussed, survival during spawning was related primarily to the ability of females to successfully deposit their eggs because a high percentage of the eggs buried were alive shortly after spawning. Survival between spawning and hatching and between hatching and emergence pertains to survival of eggs and alevins within the streambed.

The densities of live preemerged fry in the streambed of Sashin Creek in late March 1968 were 382, 260, and 108/m^2 in the upper, middle, and lower areas, respectively. From these densities I estimated a population of 2.9 million fry in the entire stream. Operation of the fry weir began just after the late March streambed sampling was

TABLE 5.—Potential egg deposition, number of live and dead eggs and alevins, ratio of live to combined live and dead eggs and alevins, and estimated survival of 1967 brood year pink salmon in three areas of Sashin Creek.

Area	Potential egg deposition per square meter		Period beginning 10 Aug. and ending	Combined live and dead eggs and alevins per square meter		Percentage of live to combined live and dead eggs and alevins		Percentage calculated survival
	Mean	90% confidence limits of mean		Mean	90% confidence limits of mean	Mean	90% confidence limits of mean	
Upper	3,947	±201	1 Oct.	1,863	±254	93	± 1	43
			1 Dec.	1,714	±295	86	± 4	37
			25 Mar.	647	±138	59	±13	10
Middle	3,672	±187	1 Oct.	1,826	±218	83	±12	41
			1 Dec.	1,591	±226	70	± 7	30
			25 Mar.	702	±147	37	± 2	7
Lower	2,644	±136	1 Oct.	1,015	±120	74	±17	28
			1 Dec.	989	±116	72	± 2	27
			25 Mar.	350	±70	31	±10	4

TABLE 6.—Percentage of estimated survival of 1967 brood year pink salmon eggs and alevins for three time periods in three areas of Sashin Creek and for the entire stream, 1967.

Area	Percentage survival			
	During spawning	Between end of spawning and hatching	Between end of hatching and emergence	Total
Upper	43	85	26	10
Middle	41	73	23	7
Lower	28	95	15	4
Entire stream[1]	37	83	22	6.8

[1]Data weighted and adjusted to include spawning grounds not included in the three study areas.

completed. Relatively few fry migrated downstream through the weir until mid-April; the daily fry migrations increased steadily through late April, reached a peak in early May, then declined rapidly, and were essentially completed by early June (Figure 1). The total number of pink salmon fry estimated to migrate from Sashin Creek from the 1967 brood year spawners was 3 million. Similar close agreements between estimates based on densities of preemerged fry and those based on number of fry counted at the weir have occurred in previous years (McNeil 1968).

The 3 million fry migrating from Sashin Creek in the spring of 1968 represent a total freshwater survival of 6.8% of the 44.4 million potential egg deposition. This is the lowest freshwater survival in the odd-year line of pink salmon spawners in Sashin Creek since 1949 (Table 1). I will subsequently attempt to show that this reduced survival was primarily due to excessive seeding of the streambed during spawning.

DISAPPEARANCE OF EGGS AND ALEVINS

To determine the number of eggs and alevins that disappeared from the streambed, I compared the potential egg deposition with the numbers of live and dead eggs at the end of spawning and the number of eggs and alevins at the time of hatching and just before emergence. In 1967, 55% of the potential egg deposition disappeared during spawning. The fate of these eggs is unknown, but they were probably removed from the stream during the spawning period by predators, scavengers, or turbulent streamflow. McLarney (1967) and McNeil (1968) discussed the roles of fish predators (especially sculpins) and water turbulence in removing eggs from Sashin Creek during spawning and between spawning and hatching.

McNeil (1968) found that eggs and alevins of the 1963 and 1965 brood years disappeared at different rates in the upper, middle, and lower study areas of Sashin Creek. Most of the 1963 brood year progeny disappeared during spawning, and most of the 1965 brood year progeny disappeared between hatching and emergence (over the winter). I will examine closely the possible fate of eggs and alevins during this period (December to March) because the factors that caused a reduced freshwater survival of 1967 brood year progeny prevailed during this period.

The estimated percentages of the potential egg deposition that disappeared in the upper, middle, and lower areas of Sashin Creek were similar within each of the three periods. This disappearance varied greatly between periods: 55% of the progeny (eggs or alevins) had disappeared by 1 October, 4% between October and December, and 25% between December and March (Table 7). The disappearance between hatching and emergence (December and March) appears more significant when expressed in terms of numbers present in December; 56-65% of the eggs and alevins in the upper, middle, and lower areas of Sashin Creek on 1 December had disappeared by 25 March (Table 8).

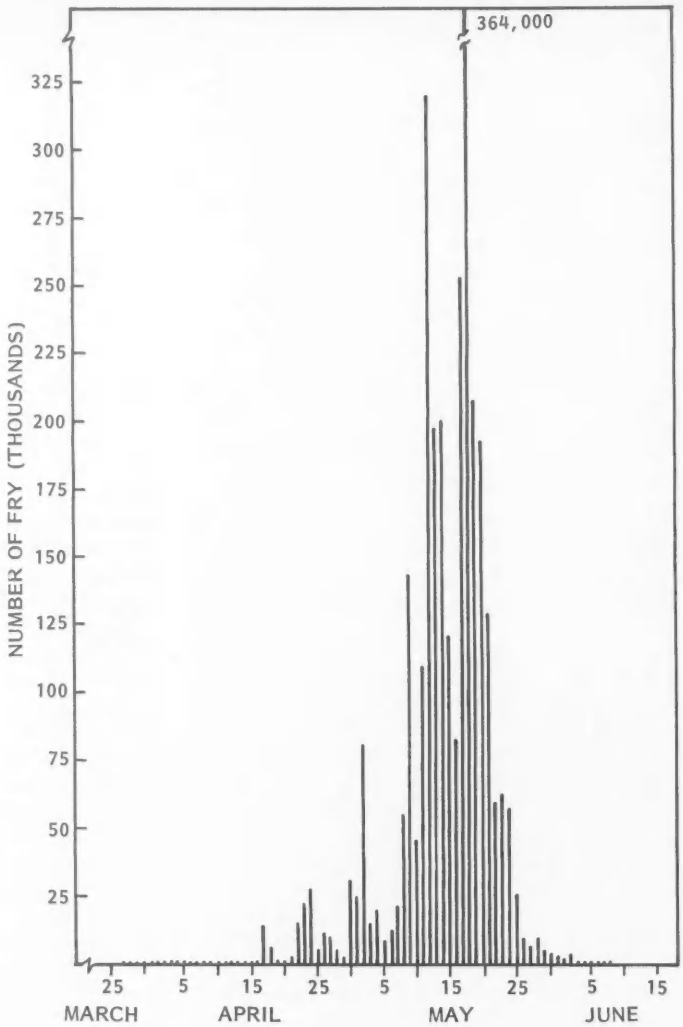

FIGURE 1.—Daily number of 1967 brood year pink salmon fry counted through Sashin Creek weir in spring 1968.

Mortality Patterns in the Streambed

Mortality of eggs and alevins within the streambed at Sashin Creek is evident in two ways: 1) as a reduction in the total population of eggs and alevins within the streambed, i.e., they disappear, and 2) as an increase in the number of dead eggs and alevins in the streambed and a decrease in the number of live eggs and alevins. In the first instance, some factors that can cause eggs and alevins to disappear are turbulent streamflow, streambed scouring, predation, and scavenging. Excluding predation, these same factors can also cause dead eggs and alevins that may have died for other reasons to disappear from the streambed. In the second instance, factors causing an increase in the number of dead eggs and alevins within the streambed are generally relatable to desiccation, freezing, and the quality of intragravel water.

In addition, dead eggs and alevins may disappear because of at least two factors that do not affect live eggs and alevins: biochemical decomposition and consumption by intragravel invertebrate scavengers. Thus, factors that cause eggs

TABLE 7.—Percentage of potential egg deposition of 1967 brood year pink salmon that disappeared from three areas of Sashin Creek and from the entire stream by 1 October 1967, 1 December 1967, and 25 March 1968.

Area	Estimated percentage of potential egg deposition disappearing		
	By 1 Oct.	1 Oct. to 1 Dec.	1 Dec. to 25 Mar.
Upper	53	4	27
Middle	50	6	24
Lower	62	1	24
Entire stream[1]	55	4	25

[1]Data weighted and adjusted to include spawning grounds not included in the three study areas.

TABLE 8.—Estimated densities of all eggs and alevins (live and dead) in three areas of Sashin Creek on 1 December 1967 and 25 March 1968, and percentage that disappeared between the two dates.

Area	Number of eggs and alevins per square meter on		Percentage that disappeared between dates
	1 Dec.	25 Mar.	
Upper	1,714	647	62
Middle	1,591	702	56
Lower	989	350	65

or alevins to disappear from streambed gravels may or may not have been the initial cause of death.

It is unlikely that turbulent streamflow, streambed shifting, or predation were the reasons that 1967 brood year eggs or alevins disappeared between early December and late March. Streamflows were generally low, and although an intermittent ice cover was present on Sashin Creek during January, February, and March, there was no indication of streambed shifting because of ice scouring. A series of short metal stakes driven into the streambed throughout the stream in November to mark coho salmon, *O. kisutch*, redds was still in place in March, indicating that no streambed shifting had occurred.

Most fish in Sashin Creek that could eat pink salmon eggs and alevins (juvenile coho salmon; rainbow trout, *Salmo gairdneri*; Dolly Varden, *Salvelinus malma*; and coastrange sculpin, *Cottus aleuticus*) are essentially dormant during the winter when water temperatures are low. Chapman and Bjornn (1969) have shown that resident stream salmonids may disappear into the substrate when water temperatures fall below 4.4 °-5.5 °C. I have observed similar behavior in Sashin Creek. Stream temperatures in Sashin Creek were below 4.4 °C from 13 December 1967 to 20 April 1968.

Water ouzels, *Cinclus mexicanus*, and mergansers, *Mergus merganser*, are occasionally present on Sashin Creek during the winter and could account for the disappearance of some eggs and alevins during open water periods. In considering the magnitude of the disappearance of 1967 brood year eggs and alevins in Sashin Creek between December and March, it is unlikely that the maximum possible loss to these sources is significant. This conclusion is based on the small numbers of mergansers and ouzels present, the amount of time the stream was covered with ice, and the large number of eggs or alevins that disappeared. Between two and five mergansers were noted in the vicinity periodically. When present, these birds spent much of their time in the intertidal portion of Sashin Creek or in the adjacent estuary. Only four of the smaller and territorial ouzels normally occur along the upper, middle, and lower areas of Sashin Creek in winter, and during periods of ice cover these birds go elsewhere. Based on periodic observations and temperature records, I estimate the stream was covered with ice approximately half the 1967-68 winter.

The estimated population of live and dead pink salmon eggs and alevins in Sashin Creek was 18.3 million on 1 December 1967 and 7.2 million on 25 March 1968 (Table 9), making a loss of 11.1 million eggs and alevins between the two dates. Because there is little evidence that the loss was caused by external factors that physically removed eggs or alevins from the streambed, the loss was likely due to factors within the intragravel environment.

The disappearance of 11.1 million eggs and alevins from the streambed between hatching and emergence led me to examine the relation between live eggs and alevins and dead eggs and alevins in the streambed. The densities of dead eggs and alevins in the upper, middle, and lower areas (Table 10) indicated that the numbers of dead eggs and alevins remained relatively stable between the time periods. This does not necessarily indicate that dead eggs in the streambed during one sampling period were still there during a later sampling period. Dead eggs can disappear at any time for many reasons, but can persist in a

TABLE 9.—Estimated population of live and dead pink salmon eggs and alevins in Sashin Creek on 1 October 1967, 1 December 1967, and 25 March 1968.

Sample date	Millions of eggs and alevins in streambed		
	Live	Dead	Total
1 Oct. 1967	16.5	3.4	19.9
1 Dec. 1967	13.7	4.6	18.3
25 Mar. 1968	3.0	4.2	7.2

streambed for as long as 18 mo (McNeil et al. 1964). Once hatching is completed, no new dead eggs can be added to the streambed. Because hatching of live eggs was well underway on 1 December (about 35% completed), many of the dead eggs present in March had already died by 1 December (Table 10).

Most of the eggs and alevins that disappeared over the winter (about 11 million; Tables 7, 8, 9) were individuals that had been alive on 1 December because the number of dead eggs and alevins was essentially unchanged from December (4.6 million) to March (4.2 million) (Table 9). Mortality (in the form of disappearance) of live eggs and alevins in the streambed between 1 December and 25 March was 74% in the upper area, 77% in the middle area, and 85% in the lower area (Table 11). Of the 11.1 million pink salmon eggs and alevins that disappeared within the streambed between 1 December and 25 March, 10.7 million were alive on 1 December.

As previously mentioned, the cause of the disappearance of dead eggs and alevins in the streambed may differ from the cause of their deaths. This apparently occurred with the 1967 brood year pink salmon progeny in Sashin Creek, and I offer the following theoretical sequence to explain the major overwinter disappearance of eggs and alevins.

The greatest number of fry produced in Sashin Creek since 1940 was 5.9 million (Table 1). On 1 December 1967, 13.7 million live pink salmon eggs and alevins were in the Sashin Creek streambed (Table 9), a number that appears to exceed the capacity of the streambed for pink salmon fry production. I postulate that the high initial density of eggs led to a severe mortality of embryos in the early alevin stage, probably because of widespread oxygen privation or a combination of oxygen privation and a buildup of toxic metabolites. The rate of oxygen consumption by embryos increases steadily with development (Wickett 1954, 1962) and coincides with the general lowering of streamflows during the late fall, followed by stabilization of streamflows at near the normal winter levels.[4] This combination of conditions permitted the embryo population to survive up to, but not much beyond, the hatching period. These recently hatched dead alevins then apparently disappeared rapidly within the streambed through the combined action of biochemical decomposition and intragravel invertebrate scavenging. As I will show later, the rapid disappearance of recently hatched dead alevins in the streambed seems consistent with this hypothesis.

Although no intragravel water quality data are available from Sashin Creek during or shortly after hatching to support the above theory, a comparison of the rates of oxygen consumption by pink salmon embryos of various ages indicates that oxygen requirements do steadily increase during the hatching period. The rates of oxygen consumption reported for early stage eggs (7-26 days old) have ranged from 0.0003 mg O_2/egg per h (Wickett 1954) to 0.0005 mg O_2/egg per h (Brickell 1971). Brickell found that the rate of oxygen consumption by 35-day-old pink salmon eggs was 0.0018 mg O_2/egg per h, almost four times the rate he measured for 7-day-old eggs. Faintly eyed 38-day-old eggs had an oxygen consumption rate of 0.002 mg O_2/egg per h (Wickett 1962) while 7-day-old alevins had a consumption rate of 0.01 mg O_2/alevin per h (Wickett 1954).

TABLE 10.—Estimated densities of dead pink salmon eggs and alevins in three areas of Sashin Creek on 1 October 1967, 1 December 1967, and 25 March 1968.

	Dead eggs and alevins per square meter					
	Upper area		Middle area		Lower area	
Date	Eggs	Alevins	Eggs	Alevins	Eggs	Alevins
1 Oct. 1967	129	0	310	0	264	0
1 Dec. 1967	223	7	459	18	266	11
25 Mar. 1968	196	69	334	108	199	43

TABLE 11.—Estimated densities of live pink salmon eggs and alevins in three areas of Sashin Creek on 1 December 1967 and 25 March 1968 and disappearance of live eggs or alevins between the two dates.

	Live eggs and alevins per square meter				Percentage of live eggs or alevins that disappeared between dates
	1 Dec. 1967		25 Mar. 1968		
Area	Eggs	Alevins	Eggs	Alevins	
Upper	899	575	0	382	74
Middle	769	345	0	260	77
Lower	463	249	0	108	85

[4]Seasonally, stream discharge in Sashin Creek is usually highest in fall and lowest in summer. Discharge in winter months may also be low, but is normally above summer levels. Because unseasonably low winter discharge could reduce oxygen delivery to embryos below the normal seasonal pattern, I compared the low monthly discharge during December, January, February, and March for 1967-68 with low discharge patterns in the same months for the period 1951-52 to 1966-67. The low mean monthly discharge from Sashin Creek during December, January, February, and March ranged from 18 to 62 ft^3/s and averaged 33 ft^3/s for the 16-yr period. The mean minimum monthly discharge during these same 4 mo in 1967-68 was 30 ft^3/s (U.S. Geological Survey 1969), suggesting that low streamflow levels during these months in 1967-68 were near normal.

In addition to the increasing oxygen requirements due to growth and development of live embryos, Brickell (1971) found that rates of oxygen consumption by dead intact pink salmon eggs exceeded those of early stage live eggs fourfold: 0.0018 mg O_2/whole dead egg per h versus 0.0004-0.0005 mg O_2/7-day-old live egg per h. He noted even greater oxygen consumption for dead eggs when the chorion was pierced or slit or the egg was fragmented: mean oxygen consumption of fragmented dead eggs in constant-flow cylinders was 0.017 mg O_2/egg per h, which exceeds the rate Wickett (1954) found for 7-day-old live alevins. It follows that alevins that die shortly after hatching, because of their soft, exposed, and readily oxidizable tissue, would have higher rates of oxygen consumption than whole intact dead eggs, live eggs, or early stage live alevins.

These increases in oxygen consumption upon death of developing pink salmon embryos are the rationale for suggesting a "snowball effect"—rapidly increasing deaths of embryos once lethal oxygen concentrations were approached. With high densities of live embryos already placing excessive demands on the oxygen and each death increasing the demand, the resulting heavy mortality could have caused fry production to plunge below that expected from lower initial egg densities—an excellent example of Neave's (1953) theory of compensatory mortality.

Disappearance of Dead Eggs Versus Disappearance of Dead Alevins

To test the hypothesis that dead alevins disappear within the streambed more rapidly than dead eggs, I conducted a small study in Sashin Creek in the winter of 1968-69 to consider the relative persistence of dead eggs and alevins in the streambed. A series of Vibert boxes (small plastic perforated containers), each containing a mixture of streambed gravel, 10 dead eggs, and 10 dead alevins (all from 1968 brood year pink salmon) were buried in Sashin Creek on 14 December 1968. The boxes were buried about 20.3 cm deep across a riffle in the middle study area. At irregular intervals, pairs of the boxes were removed from the streambed and the contents were preserved for examination.

Alevins disappeared from the Vibert boxes at a much faster rate than eggs (Table 12). Fewer than half of the original number of alevins were still recognizable at the end of 2 wk; after 37 days only one box contained identifiable alevins. Although the dead alevins disappeared rapidly, only a few of the dead eggs disappeared. In a study to determine whether certain stonefly numphs were predators or scavengers on salmon eggs and alevins, Ellis (1970) found in one experiment that dead pink salmon alevins buried in Vibert boxes in a stream essentially disappeared within a 2-wk period.

TABLE 12.—Contents of Vibert boxes with dead pink salmon eggs and alevins buried in Sashin Creek streambed between 14 December 1968 and 14 April 1969.[1]

No. of days buried	Eggs recovered	Alevins recovered	Invertebrates recovered	
			Insect larvae[2]	Planarian worms[3]
0	20	20	0	0
9	20	10	14	4
16	20	4	37	20
24	20	2	40	34
30	20	1	27	144
37	20	4	36	11
44	20	0	55	5
51	19	0	70	3
71	19	0	196	4
86	20	2	72	9
96	20	0	135	6
109	20	0	149	29
121	19	0	102	36

[1]Each box originally contained 10 dead eggs and 10 dead alevins. Two boxes were removed on each sample date and the contents combined for reporting.
[2]Of all insect larvae recovered, 80% were Plecoptera, 16% Diptera, 3% Trichoptera, and 1% Ephemeroptera.
[3]Tentatively identified as *Polycelis borealis*, a species that Kenk (1953) commonly found in clear cold streams in southern parts of Alaska.

Concurrently with the rapid disappearance of dead alevins from the buried boxes was a rapid buildup of invertebrates in the boxes. Although invertebrates are commonly found with salmon embryos (Briggs 1953; McDonald 1960; Nicola 1968), it is frequently impossible to determine if predation or scavenging is occurring. Although some groups of stonefly nymphs are known to attack live salmon embryos (Stuart 1953; Claire and Phillips 1968), Ellis (1970) concluded that nymphs of the carnivorous genus *Alloperla* were basically scavengers rather than predators.

In addition to various insect larvae, a planarian worm tentatively identified as *Polycelis borealis* was commonly found in the boxes buried in Sashin Creek (Table 12). Little is known on the biology or life history of this planarian, but under favorable conditions it appears to rapidly increase its numbers in the streambed, and thus may be particularly important in removing dead alevins. I have observed successive seasonal increases in the relative abundance of planarians in samples taken from the Sashin Creek streambed with the hydraulic sampler in the fall, winter, and spring. Total counts of planarians removed from the streambed with the hydraulic sampler are not pos-

sible,[5] but partial counts indicated that by March the densities of planarians in some parts of Sashin Creek commonly reached several thousand per square meter. A similar seasonal increase in streambed populations of planarians concomitant with the seasonal occurrence of sockeye salmon, *O. nerka*, embryos has been noted elsewhere.[6]

In Sashin Creek there is little doubt that high planarian populations are related to the presence of salmon eggs and alevins, because planarians are scarce in streambed gravels above the impassable falls where salmon do not spawn. However, the precise role of these organisms in the ecology of spawning beds is unknown. To learn something about the role of planarians, I conducted tests with various combinations of planarians and live and dead salmon eggs and alevins in experimental containers. In these tests planarians did not prey on and were not toxic to live embryos, nor did they feed on dead eggs unless the chorion was broken and the egg contents exposed.

EVIDENCE OF OVERSEEDING

In assessing the probability of streambed overseeding in Sashin Creek in the 1967 brood year, it is most useful to compare fry production in 1967-68 with production in other years. Since 1940, production has varied from 50 fry to almost 6 million fry; corresponding parent escapements varied from 8 to 92,085 (Table 1). Only three escapements exceeded that of 1967, and only one of these (1940) produced more fry (about 0.4 million more) (Table 1). When the numbers of fry are plotted against potential egg deposition, a dome-shaped fry production curve is derived for Sashin Creek (McNeil 1969). The relative position of fry production for the 1967 brood year falls near the descending limb of the curve; fry production from the 1941 and 1942 brood years indicates a continuing decrease in fry production as escapements increased (Figure 2).

Data collected since 1961 on the density of eggs in the three study areas at the end of spawning provide a means of more precisely defining the fry production potential of the stream. Plotting fry production as a function of actual egg deposition for each area produces curves that suggest the potential maximum fry production in the upper and middle areas is around 500 fry/m² and the potential in the lower area is about half that number (Figure 3). In 1967 the actual density of eggs deposited considerably exceeded twice the theoretical maximum fry production in all three areas and the fry production was considerably below the maximum; it appears that overseeding occurred in 1967.

Until 1967 the timing of entry of adults into Sashin Creek had usually been an accurate indicator of the freshwater survival of progeny (Merrell 1962; McNeil 1968; Ellis 1969). The presumed biological basis for the correlation between early spawning and high survival was that embryos de-

[5]When large numbers of planarians are excavated with the hydraulic sampler, many elongate their bodies and pass through the meshes of the collecting net.

[6]W. L. Hartman, W. R. Heard, and C. W. Strickland. 1962. Red salmon studies at Brooks Lake biological field station, 1961. Unpubl. manuscr. on file, NWAFC Auke Bay Lab. NMFS, NOAA, P.O. Box 155, Auke Bay, Alaska.

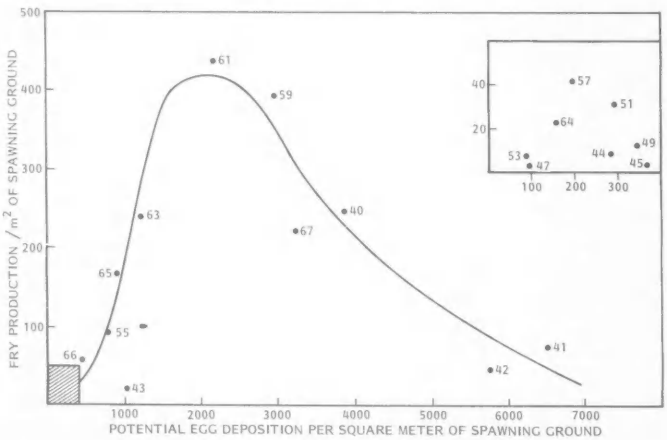

FIGURE 2.—Production of pink salmon in Sashin Creek, 1940-67. The shaded area in the lower left is shown on a larger scale in the upper right corner. Nine generations of the even-year line 1946-62 were excluded because fry productions were all $<1/m^2$. Adult escapement in these years was correspondingly low. The curve (modified from McNeil 1969) is fitted by eye.

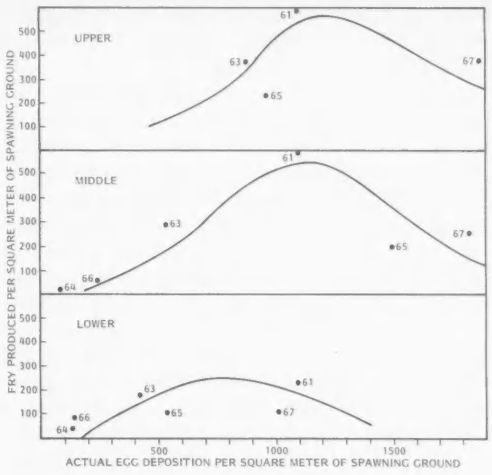

FIGURE 3.—Production curves for pink salmon in three study areas of Sashin Creek, 1961-67, showing relation between number of eggs in the streambed at the end of spawning and number of fry produced. Spawning did not occur in all areas in all years. Location of the 1961 point on the abscissal axis is not precise: success of spawning that year was based on subjective estimates (see McNeil et al. 1964). Curves are fitted by eye.

veloping initially at warmer temperatures had a survival advantage over those developing initially at cooler temperatures (Merrell 1962). In Sashin Creek, spawning closely follows the time of entry into the stream, so that early entry implies early spawning. Although the 1967 spawners entered Sashin Creek on the second earliest date on record, freshwater survival fell well below the predicted level (Figure 4). From the predicted freshwater survival of about 18% shown in Figure 4, the 1967 spawners should have produced 8 million fry.

On the basis of the relation of survival to time of spawning, McNeil (1969) suggested the dome-shaped freshwater production curve for Sashin Creek (Figure 2) may be the result of large escapements, more superimposition, and replacement of the more viable eggs from early spawning by less viable eggs from later spawning. From evidence available, there is little doubt that in Sashin Creek, progeny from early spawners have survival advantages over progeny from late spawners. I suggest, however, that when escapements are large, a point is reached where the number of eggs in the streambed determines ultimate survival, regardless of when spawning occurs.

The local climate and its resulting effects in the stream are extremely variable and have a marked influence on what actually constitutes an overseeded spawning bed at a specific time. Climate influences efficiency of spawning through variations in streamflows, so that overseeding does not occur at a fixed number of spawners. Similarly, streambed overseeding results from a dynamic interaction between the density of eggs in the gravel, certain ecological characteristics that define the fry production capability of the streambed, and prevailing climatic influences on the intragravel environment during the 6 to 8 mo eggs and alevins are in the streambed. Overseeding of streambed gravels will occur at lower egg densities when climatic influences (rainfall, stream discharge, ice cover, etc.) are more adverse to the intragravel environment.

Perhaps the most convincing evidence of streambed overseeding in Sashin Creek is the seasonal change in instantaneous (monthly) mortality coefficients of the 1963, 1965, and 1967 brood

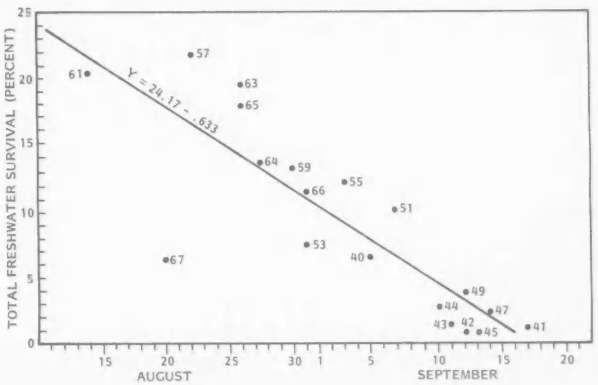

FIGURE 4.—Relation of freshwater survival of pink salmon in Sashin Creek to date when 50% of spawners had entered the stream. Data are from period 1940 to 1967; escapements <1,000 adults are excluded. The curve $Y = 24.17 - 0.633X$ fitted by least squares, where $X = 0$ corresponds to 10 August. Numbered points identify brood years (modified from McNeil 1968).

year progeny (Figure 5). Mortality coefficients for 1963 and 1965, the only years besides 1967 when estimates of live eggs and alevins were made after spawning, at hatching, and before emergence, are from McNeil (1968); the equation and notation for computing the instantaneous mortality coefficients for the 1967 brood year follow McNeil (1966). Time intervals assigned the three periods were 1.4 mo (from potential egg deposition through spawning), 2.0 mo (from spawning to hatching), and 3.7 mo (from hatching to emergence). The survival percentages by time periods are given in Table 6.

The impact of the heavy mortality between hatching and emergence in 1967 brood year progeny is evident in Figure 5. Monthly mortality coefficients during spawning were also high in 1963 and 1967 (0.76 and 0.71); the lower mortality during spawning in 1965 (0.31) probably reflects efficient spawning during the low streamflow condition prevailing that year (McNeil 1968). Mortality from spawning to hatching was similar, but mortality from hatching to emergence was strikingly different in each of the 3 yr (Figure 5). McNeil (1968) suggested the increase in overwinter mortality of 1965 brood year progeny (0.26) over 1963 brood year progeny (0.07) might have been related to a delayed mortality from low concentrations of dissolved oxygen in early embryo development during drought conditions in late summer and early fall in 1965. The number of spawners in 1967 was more than double the number in 1963 and 1965 (Table 1). The overwinter mortality of 1967 brood year progeny (0.42) was considerably higher than the high mortality of the 1965 brood year (0.26). The heavy overwinter mortality experienced by the 1967 brood year progeny may also have been caused by low dissolved oxygen concentrations. However, because no drought conditions existed while the progeny were in the gravel, these poor oxygen conditions probably resulted from the high density of eggs and alevins in the streambed.

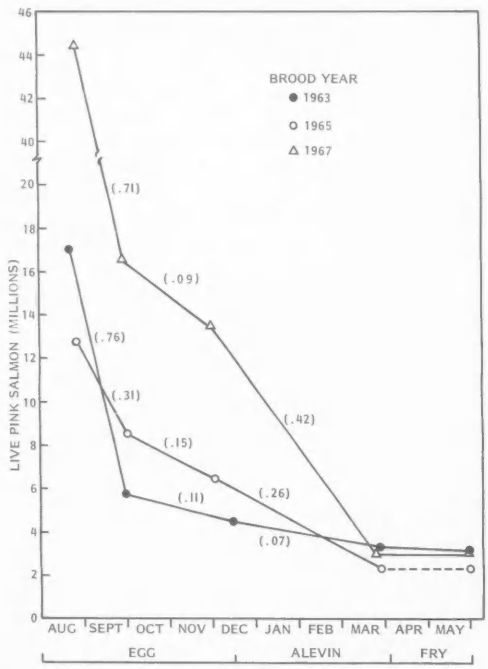

FIGURE 5.—Number of live pink salmon in Sashin Creek at the beginning and end of three periods in freshwater for 1963, 1965, and 1967 brood years. Numbers in parentheses show instantaneous monthly mortality coefficients from the egg through alevin stages. Mortality during fry migration (April and May) for the 1963 and 1967 brood years was negligible when measured as the difference between streambed and weir estimates of total fry production. The dotted extension of the 1965 brood year assumes no mortality during this period.

SUMMARY

1. In 1967, 38,067 pink salmon spawned in Sashin Creek on Baranof Island, Alaska. Fifty-two percent of the spawners (19,639) were females; mean fecundity was 2,260 eggs/female and the potential number of eggs available for deposition totaled 44.4 million.

2. Entry of spawners into the stream was the second earliest on record; based on the previously consistent relation between time of entry and freshwater survival, the production of fry should have been greater than any previously recorded, but the 3 million fry produced were less than half the predicted number.

3. Mean female densities on the spawning grounds were 1.74/m² in the upper area, 1.62/m² in the middle area, and 1.17/m² in the lower area. Densities were higher in the upper area at the beginning of spawning before significant levels of spawning occurred in the middle or lower areas. The tendency for spawners in the odd-year line to utilize the upper area of Sashin Creek may be due to genetic factors, including timing of escapements, and possibly differential marine survival favoring fry produced in the upper area.

4. Survival of progeny of the 1967 spawners was determined a) from stream entry to end of spawning, b) from end of spawning to hatching, c) from hatching to shortly before fry emergence, and d) from shortly before emergence to emergence and downstream migration of fry. In general, survival in each of these time periods was greatest in the upper area, lowest in the lower area, and intermediate in the middle area, a pattern consistent with previous survival studies at Sashin Creek. Total freshwater survival from potential egg deposition to preemerged fry was 10%, 7%, and 4% in the upper, middle, and lower areas, respectively, and 6.8% for the entire stream. The total number of migrating fry agreed closely with the estimates of preemerged fry in the streambed in late March.

5. Mortality of eggs and alevins was high during spawning, low between spawning and hatching, and high between hatching and emergence. Between 1 December 1967 and 25 March 1968, 11.1 million eggs or alevins disappeared within Sashin Creek streambed; 10.7 million of these were alive on 1 December. The high densities of eggs and alevins in the streambed after spawning and at hatching are believed to exceed the streambed capacity for fry production. High overwinter mortalities appear to have occurred shortly after hatching, probably from critical levels of dissolved oxygen in intragravel water. Critical oxygen levels apparently developed under average winter streamflow conditions due to the high biochemical oxygen demand placed on the streambed by high egg and alevin densities.

6. Recently hatched dead alevins disappear rapidly within the streambed because of biochemical decomposition and invertebrate scavenging. In comparison with dead alevins, dead eggs disappear slowly. In Sashin Creek, insect larvae and a planarian, probably *Polycelis borealis*, may be particularly important in removing dead salmon eggs and alevins from the streambed.

7. Several aspects of the historical patterns of pink salmon fry production in Sashin Creek suggest that streambed overseeding occurred in 1967. Fry production from the 1967 spawners falls on the descending limb of the fry production curves, both for the stream as a whole (since 1940) and for the individual stream areas (since 1961). From the historical pattern of time of adult entry and resulting freshwater survival, freshwater survival of 1967 brood year progeny should have been around 18% (or a production of 8 million fry). Survival of progeny during spawning and between spawning and hatching was adequate to reach these predicted levels. Overwinter mortalities (between hatching and emergence), however, were higher than any previously recorded. Compensatory losses during this period were probably due to the presence of too many eggs and alevins in the gravel for existing environmental conditions—streambed overseeding.

8. Overseeding does not invariably occur at some precise density of eggs, but rather is a dynamic interaction between densities of eggs and alevins in the gravel, certain ecological characteristics that define the fry production capability of the streambed, and the prevailing climatological features during the 6- to 8-mo period eggs and alevins reside in the streambed.

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VERTICAL DISTRIBUTION AND PHOTOSENSITIVE VESICLES OF PELAGIC CEPHALOPODS FROM HAWAIIAN WATERS

RICHARD EDWARD YOUNG[1]

ABSTRACT

Vertical distribution data were obtained for 47 species of pelagic cephalopods off Oahu, Hawaii. Peaks in species richness occurred at 500-800 m during the day and in the upper 300 m at night. Over 80% of the individuals occurred in the upper 250 m at night. Approximately 60% of the species underwent diel vertical migration, and most of these migrated into the upper 250 m. In five of nine groups of closely related species, clear differences in habitat were found.

Deepwater spawning appeared to occur in a variety of cephalopods. Two of the bathypelagic octopods brooded their young at or above the upper limit of the remaining adult population. In doing so, the extent of the upward migration of newly hatched individuals was reduced.

Photosensitive vesicles occurred in all species. These organs probably detect downwelling daylight for regulating vertical migration and counterillumination. The vesicles also appeared to form an elaborate system for monitoring bioluminescent light from the animal's own photophores, from within the mantle cavity, and from other animals located outside the visual field.

Cephalopods must occupy a wide variety of ecological roles in the pelagic realm of the open ocean: the highest diversification of families and genera is found in this environment. In order to understand these roles, the vertical distribution of these animals must be determined. A number of papers have treated various aspects of the vertical distribution of oceanic cephalopods (e.g., Pearcy 1965; Clarke 1969; Roper 1969; Gibbs and Roper 1971; Clarke and Lu 1974, 1975; Lu and Clarke 1975a, b; Roper and Young 1975). Their vertical habitats, however, remain poorly known.

Data on the vertical distribution of cephalopods is difficult to obtain: many species are uncommon, and some avoid small trawls. In this study an opening-closing net (modified Tucker trawl) provided unambiguous depth data, and a slightly larger open net (3-m Isaacs-Kidd midwater trawl) added considerable additional data; nevertheless, fast-swimming species were poorly sampled.

Extraocular photoreceptive organs, the photosensitive vesicles, were examined in each species for clues that would indicate the role of light in regulating vertical distribution patterns. The organs in squid, known as the parolfactory photosensitive vesicles, lie near the brain within the confines of the cephalic cartilage. In octopods the organs, known as epistellar photosensitive vesicles, lie within the mantle cavity adjacent to the stellate ganglia. The photosensitive vesicles are paired organs. Each organ, as the name implies, is generally composed of a large number of small vesicles. The individual vesicles contain photosensitive cells similar to those of the retina, and their photoreceptive nature has been well established (Nishioka et al. 1966; Mauro and Baumann 1968; Mauro 1977). The specific functions of the photosensitive vesicles are unknown in both neritic and oceanic cephalopods although many suggestions have been made (see Packard 1972).

Several papers discussing the relationship of vertical distribution to eye structure, bioluminescence and/or development of photosensitive vesicles in selected species have already appeared (Young 1972a, 1973, 1975a, c, d, 1977). Some data on distribution taken during the initial phases of this program have been published by Roper and Young (1975). This paper examines the vertical distribution of all pelagic cephalopods taken off Hawaii and the morphology and orientation of their photosensitive vesicles.

MATERIALS AND METHODS

Specimens were collected off the island of Oahu in the Hawaiian archipelago at long. 158°20′W, lat. 21°20′N over depths between 1,500 and 4,000 m. Collections were made from September 1969 to November 1974 primarily from the RV *Teritu*. Over 3,300 specimens were taken in horizontal tows during about 1,000 h of trawling time.

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Cephalopods were collected primarily with two types of nets: a 3-m opening-closing modified Tucker trawl and a 3-m Isaacs-Kidd midwater trawl (IKMT). Details of the trawling with the Tucker trawl are given by Walters (1976). When the Tucker trawl failed to close or close completely, the trawl was considered an open tow. Tows usually were made at 5 to 6 km/h for a period of 3 h. Twilight periods were generally avoided. Tows made with net closed indicated the catch contained almost no contamination. Contamination from previous tows was minimized by carefully cleaning the net after each tow. The trawl tended to wander vertically when open; this was most severe in deep tows. During the latter part of the program, acoustic depth telemeters allowed trawl depths to be continuously adjusted and greatly reduced wandering. The distribution figures indicate the extent of this wandering. Trawl depths usually were determined with a time-depth recorder attached to the trawl.

Clarke (1973) discussed trawling methods with the IKMT. The trawl was lowered quickly then towed horizontally at 5 to 6 km/h for usually 2 h. Retrieval was rapid with the ship moving slowly ahead. Vertical wandering of the net was not as serious as with the Tucker trawl. All specimens captured with the IKMT were assumed to come from the modal trawling depth of the net, or if no clear mode was present, from the midpoint of the effective vertical range of the tow. The occasional capture of a specimen during setting or retrieval of a net results in an anomalous depth record below the animal's normal habitat. Contamination of the catch by animals from previous tows occasionally occurred with the IKMT. This contamination is especially serious as the error may be impossible to detect.

IKMT data for a few of the most abundant species are presented both as catch per trawling effort and as actual catch figures (Table 1). The remaining distribution figures are designed to show animal size vs. depth relationships and to indicate the precision and reliability of the data (e.g., fishing range of the tow, open or opening-closing tow). As a result, corrections in the data for unequal sampling at various depths could not be made. This bias was especially critical at depths <400 m during the day and at depths >1,000 m during the day and night where sampling was low. The magnitude of this error can be determined from Table 2, which lists sampling time in each 100-m depth interval.

Depth data for most species taken over the entire trawling period have been combined. Therefore, short-term variation in depth distributions may be obscured. Where sufficient data exist to determine general distribution patterns based on Tucker trawls alone, these data are presented separately. For species with insufficient data, data from both trawls are combined in the figures. In most cases larvae, which usually have a different vertical distribution than adults, have been excluded from the distribution figures and the

TABLE 1.—Depth distribution, capture rates, and numbers of the most abundant cephalopod species captured by the Isaacs-Kidd midwater trawl. Day captures for *Pterygioteuthis giardi* are included in Figure 4. R = capture rate in numbers per 1,000 m^3 of water sampled. N = actual number captured. ND = no data.

	Day						Night							
	Abralia sp. B		*Pterygioteuthis microlampas*		*Pyroteuthis addolux*		*Abralia* sp. B		*Pterygioteuthis microlampas*		*Pyroteuthis addolux*		*Pterygioteuthis giardi*	
Depth (m)	R	N	R	N	R	N	R	N	R	N	R	N	R	N
0-50	ND	ND	ND	ND	ND	ND	5.4	14	15.2	39	1.5	4	5.8	15
50-100	ND	ND	ND	ND	ND	ND	17.9	52	62.1	180	6.5	19	7.9	23
100-150	ND	ND	ND	ND	ND	ND	3.2	8	23.3	57	7.3	18	2.0	5
150-200	0	0	0	0	0	0	5.2	14	14.1	38	15.9	43	2.2	6
200-250	0	0	0	0	0	0	1.0	1	0	0	3.1	3	0	0
250-300	ND	ND	ND	ND	ND	ND	1.0	1	1.0	1	6.5	6	4.3	4
300-400	3.0	4	2.3	3	6.9	9	0	0	0	0	0	0	0	0
400-500	10.9	14	42.3	54	14.1	18	4.9	3	4.9	3	4.9	3	0	0
500-600	7.4	9	72.2	87	20.7	25	3.4	2	6.9	4	5.1	3	0	0
600-700	22.8	26	8.7	10	14.9	17	0	0	1.4	1	0	0	0	0
700-800	1.0	2	5.3	10	3.2	6	2.8	3	0	0	0	0	0	0
800-900	3.6	3	8.5	7	1.2	1	0	0	0	0	0	0	0	0
900-1,000	2.1	2	1.0	1	2.1	2	0	0	0	0	0	0	0	0
1,000-1,100	1.5	1	20.1	13	1.5	1	0	0	0	0	5.4	1	0	0

TABLE 2.—Trawling time in minutes. Since trawls of two different sizes were used, a correction factor of 0.6 was applied to the trawling times of the Tucker trawl to compute the adjusted total trawling time. This factor represents the approximate difference in effective mouth areas of the two nets. Open tows = time of each tow was assigned to one depth. Opening-closing tows = time of each tow was apportioned among depth zones traversed by the trawl. IKMT = Isaacs-Kidd midwater trawl.

	Tucker trawl				IKMT		Total adjusted to IKMT	
	Open		Opening-closing		Open			
Depth (m)	Day	Night	Day	Night	Day	Night	Day	Night
0-50		1,091		939		2,562		3,780
50-100	180	1,112		614		2,897	108	3,932
100-150		781	27	591		2,442	16	3,265
150-200	144	530	84	870	130	2,689	267	3,529
200-250		536	186	320	177	944	289	1,458
250-300	146		31	871		911	106	1,434
300-350	180		203	514	452	605	682	913
350-400	180	180	460	407	839	552	1,223	904
400-500	360	502	1,529	1,413	1,276	605	2,409	1,754
500-600		376	1,748	927	1,204	577	2,253	1,359
600-700		133	1,683	1,420	1,139	714	2,149	1,646
700-800	313	220	1,638	838	1,862	1,052	3,033	1,687
800-900			1,244	519	820	179	1,566	490
900-1,000	180	30	709	184	917	179	1,450	307
1,000-1,100		182	464	64	646	182	924	330
1,100-1,200	195		230	156	180	195	435	289
1,200-1,300	200	300	380		180		528	180
1,300-1,400	10	256	234	98			146	212
1,400-1,500			67	106			40	64
1,500-1,600				30				18
1,600-1,700			8	38			5	23
1,700-1,800			104	267			62	160
1,800-1,900			84	228			50	137
1,900-2,000			48	28			29	17
2,000-2,100			15	27			9	16
2,100-2,200			72	29			43	17
2,200-2,300			43	33			26	20
2,300-2,400				8				5

text. Specimens captured during twilight periods, with a few exceptions, have also been excluded from the charts.

Species examined are listed in Table 3. Larvae or juveniles of several additional species were captured but are not included in this study. These are: *Tremoctopus violaceus*, *Argonauta* sp., *Cranchia scabra*, *Thysanoteuthis rhombus*, *Onykia* sp. One pelagic species reported from Hawaii by Berry (1914), *Iridoteuthis iris*, was not taken. This species belongs in the genus *Nectoteuthis* and probably lives in association with the ocean floor.[2]

Photosensitive vesicles of most species were sectioned. Material was fixed either in glutaraldehyde-osmium tetroxide or Bouin's solution and was embedded in Epon 812[3] or paraffin. All vesicles sectioned contained cells with photosensitive processes and, therefore, appeared to be functional. In only a few cases did the general histology of the organs add to our understanding of their function. As a result, histological details are not included for most species.

In order to quantify the size of vesicles, an attempt was made to obtain dry weights. Many types of vesicles proved difficult to remove and clean completely. Vesicles from a series of similar-sized *Pyroteuthis addolux*, which are easily removed, were weighed and found to vary by a factor of 1.5. Because of the large individual variations and inaccuracies due to difficulties in isolating many types of vesicles, this method of quantification was abandoned. As a result, camera lucida drawings of photosensitive vesicles provide the only measure of organ size: their relative size can be approximately determined by comparison with the brain size.

RESULTS

Pyroteuthis addolux Young 1972

Vertical Distribution

During the day, 39 specimens captured by the Tucker trawl indicate a vertical range for this

[2]Roper, C., and R. Young. Review of the Heteroteuthinae. Unpubl. manuscr.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 3.—Species of cephalopods considered.

Order Teuthoidea
- Family Enoploteuthidae
  - *Pyroteuthis addolux* Young 1972
  - *Pterygioteuthis microlampas* Berry 1913
  - *Pterygioteuthis giardi* Fischer 1895
  - *Abralia trigonura* Berry 1913
  - *Abralia astrosticta* Berry 1909
  - *Abraliopsis* sp. A, n.sp. being described by L. Burgess
  - *Abraliopsis* sp. B, n.sp. being described by L. Burgess
  - *Abraliopsis* sp. C, n.sp. being described by L. Burgess
  - *Enoploteuthis* sp. A, n.sp. being described by L. Burgess
  - *Enoploteuthis* sp. B, n.sp. being described by L. Burgess
  - *Thelidioteuthis alessandrinii* (Verany 1851)
- Family Ommastrephidae
  - *Symplectoteuthis oualaniensis* (Lesson 1830)
  - *Hyaloteuthis pelagicus* (Bosc 1802)
  - *Nototodarus hawaiiensis* (Berry 1912)
- Family Histioteuthidae
  - *Histioteuthis dofleini* (Pfeffer 1912)
  - *Histioteuthis celetaria pacifica* (Voss 1962)
  - *Histioteuthis* sp. under study by N. Voss
- Family Neoteuthidae
  - *Neoteuthis* sp.
- Family Bathyteuthidae
  - *Bathyteuthis abyssicola* Hoyle 1885
- Family Ctenopterygiidae
  - *Ctenopteryx siculus* (Verany 1851)
- Family Onychoteuthidae
  - *Onychoteuthis compacta* (Berry 1913)
- Family Octopoteuthidae
  - *Octopoteuthis nielseni* Robson 1948
- Family Cycloteuthidae
  - *Cycloteuthis serventyi* Joubin 1919
  - *Discoteuthis laciniosa* Young and Roper 1969
- Family Brachioteuthidae
  - *Brachioteuthis* sp.
- Family Chiroteuthidae
  - *Chiroteuthis* n.sp., being described by Roper and Young
  - *Chiroteuthis picteti* Joubin 1894
  - Chiroteuthidae n.gen., n.sp. being described by Roper and Young
  - *Planktoteuthis lippula* (Chun 1908)
  - *Grimalditeuthis bomplandi* (Verany 1837)
- Family Mastigoteuthidae
  - *Mastigoteuthis famelica* (Berry 1909)
  - *Mastigoteuthis inermis* Rancurel 1972
- Family Joubiniteuthidae
  - *Joubiniteuthis portieri* (Joubin 1912)
- Family Cranchiidae
  - *Liocranchia valdiviae* (Chun 1906)
  - *Liocranchia reinhardti* (Steenstrup 1856)
  - *Leachia pacifica* (Issel 1908)
  - *Phasmatopsis fisheri* (Berry 1909)
  - *Taonius pavo* (LeSueur 1821)
  - Sandalops melancholicus Chun 1906
  - *Helicocranchia beebei* Robson 1948
  - *Bathothauma lyromma* Chun 1906

Order Octopoda
- Family Bolitaenidae
  - *Eledonella pygmaea* Verrill 1884
  - *Japetella diaphana* Hoyle 1885
- Family Amphitretidae
  - *Amphitretus pelagicus* Hoyle 1885
- Family Vitreledonnelidae
  - *Vitreledonnella richardi* Joubin 1918

Order Vampyromorpha
- Family Vampyroteuthidae
  - *Vampyroteuthis infernalis* Chun 1903

Order Sepioidea
- Family Sepiolidae
  - *Heteroteuthis hawaiiensis* (Berry 1909)

species of 375 to 510 m; most captures came from 450 to 500 m (Figure 1). IKMT data lumped into 100-m increments show most day captures between 400 and 700 m (Table 1). At night, 38 of the 41 specimens captured by the Tucker trawl indicate a vertical range of about 110 to 225 m; most specimens came from 150 to 200 m. Three specimens were captured during the night in opening-closing tows near their day habitat at depths between 360 and 480 m. Each of these three specimens was taken in a separate tow during a cruise in November 1972 within a few days of new moon. Although the upper 200 m was not sampled on this cruise, these captures indicate that at least part of

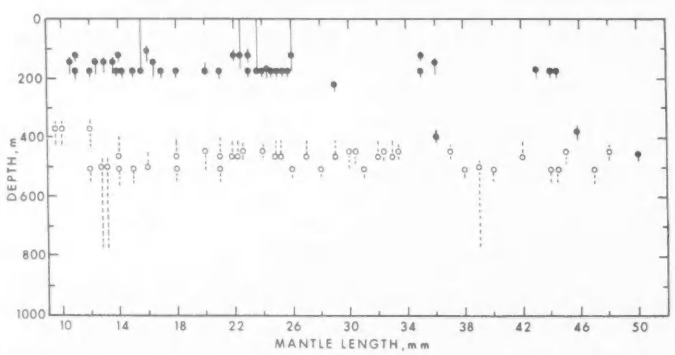

FIGURE 1.—Vertical distribution of *Pyroteuthis addolux*. Symbols for Figure 1 and subsequent figures: open circles represent day captures; closed circles represent night captures. A bar with a circle indicates an opening-closing tow with the bar representing the depth range of the tow and the circle the most likely depth of the capture (the modal depth, or if no clear mode is present, the midpoint of the vertical range of the tow). A circle without a bar indicates a capture in an open tow. A bar without an associated symbol indicates an open oblique tow. Such bars do not always intersect the zero depth line as some gradual oblique tows were made between specific depths. Solid bars represent night captures. Dashed bars represent day captures. A small dot represents a presumed contaminant.

the population was not migrating during this period. IKMT data lumped into 50-m increments show that most night captures were made between 50 and 200 m with peak catches between 150 and 200 m.

Photosensitive Vesicles (Figure 2A)

The organs are very similar to those described by R. E. Young (1977) in *Pterygioteuthis microlampas*. *Pyroteuthis addolux* has two sets of organs. The dorsal organs (the more dorsal set) lie embedded in the posterodorsal wall of the cephalic cartilage and adjacent to the optic lobes of the brain. Each ventral organ lies deeply embedded in the posteroventral surface of the cephalic cartilage. Except for a thin medial extension on each ventral organ, all organs are thick, compact, and approximately circular to square in outline. The histological structure of the dorsal and ventral organs is similar. The integument adjacent to both the dorsal and ventral organs lacks pigment and thereby forms distinctive "windows" for the passage of light.

Nerves from both dorsal and ventral organs enter the peduncle complex of the brain and their fibers disperse in the base of the peduncle lobe near its broad junction with the olfactory lobe.

Pterygioteuthis microlampas Berry 1913

Vertical Distribution (Figure 3)

The vertical distribution has been described by R. E. Young (1977). During the day, 48 specimens captured with the Tucker trawl indicate a depth range of 450 to 575 m; 85% of the specimens were taken between 450 and 500 m. IKMT data lumped into 100-m increments (Table 1) show most day captures between 400 and 600 m. At night 56 specimens taken by the Tucker trawl indicate a depth range of 25 to 180 m; nearly 85% of the captures were made between 50 and 105 m. IKMT data lumped into 50-m increments indicate a range of 0 to 200 m with a strong peak in the 50- to 100-m depth zone. The night distribution was not affected by moonlight (R. E. Young 1977).

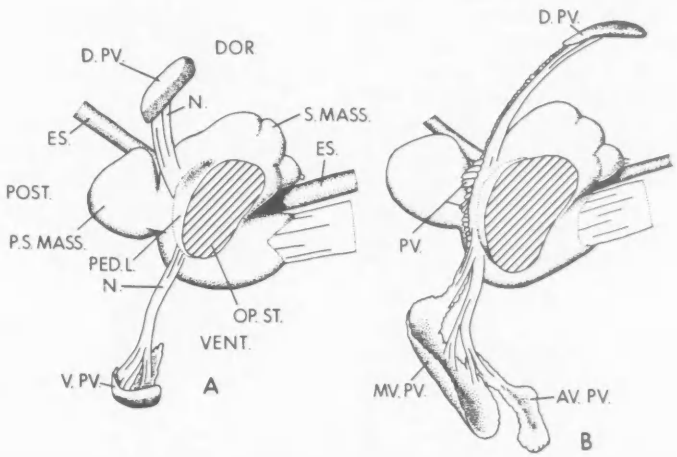

FIGURE 2.—A. Photosensitive vesicles of *Pyroteuthis addolux*. This illustration and most subsequent drawings show a side view of the brain. The optic stalk has been cut (as indicated by cross-hatching) and the optic lobe removed. The esophagus can be seen passing through the brain. Three major subdivisions of the brain are apparent (i.e., the supraesophageal mass, the posterior subesophageal mass, and the middle subesophageal mass.) A large nerve tract which extends anteriorly to the anterior subesophageal mass was cut (indicated by dotted line) and the latter portion of the brain is not shown. B. Photosensitive vesicles of *Abraliopsis* sp. B. Abbreviations for Figure 2 and subsequent figures of photosensitive vesicles: AV. PV.—Anteroventral photosensitive vesicles; C. PV.—central photosensitive vesicles; DOR.—dorsal; D. PV.—dorsal photosensitive vesicles; ES.—esophagus; GILL—gill; H. RET. M.—head retractor muscles; INT.—intestine; M. S. MASS—middle subesophageal mass of the brain; MV. PV.—midventral photosensitive vesicles; N.—nerve; OP. ST.—optic stalk; PED. L.—peduncle lobe; PIG. S.—pigment screen; POST.—posterior; P. PV.—posterior photosensitive vesicles; P. S. MASS—posterior subesophageal mass of the brain; PV.—Photosensitive vesicles; V. PV.—ventral photosensitive vesicles; S. MASS—supraesophageal mass of the brain; VENT.—ventral.

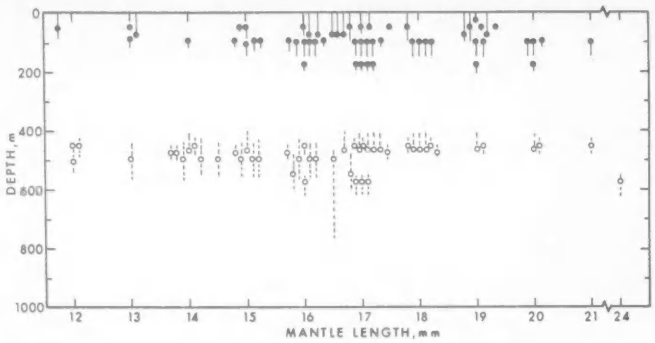

FIGURE 3.—Vertical distribution of *Pterygioteuthis microlampas*. From R. E. Young (1977). Symbols as in Figure 1.

Photosensitive Vesicles

The organs have been described by R.E. Young (1977). They are essentially the same as in *Pyroteuthis addolux*.

Pterygioteuthis giardi Fischer 1895

Vertical Distribution (Figure 4)

During the day 30 specimens captured from both trawls indicate a depth range from about 390 to 525 m; over 90% of the captures were made between 390 and 450 m. One IKMT tow captured eight badly damaged specimens at 630 m, well below their zone of maximum abundance. The previous tow had captured six specimens at 390 m that were in excellent condition; specimens from the deeper tow probably are contaminants. The depth distribution of this species may be biased by the relatively low sampling effort between 350 and 400 m.

At night, 39 captures with the Tucker trawl indicate a depth range of 15 to 180 m; over 75% of the specimens came from 15 to 50 m. IKMT data lumped into 50-m increments (Table 1) show the maximum abundance at depths of 0 to 100 m.

Photosensitive Vesicles

The organs are essentially the same as in *Pyroteuthis addolux*.

Abralia trigonura Berry 1913

Vertical Distribution (Figure 5)

Fifty specimens were captured by both trawls. Excluding presumed contaminants, the day captures were made between 390 and 650 m with nearly 80% between 450 and 560 m. At night captures were made between 30 and 200 m with over 75% between 50 and 100 m.

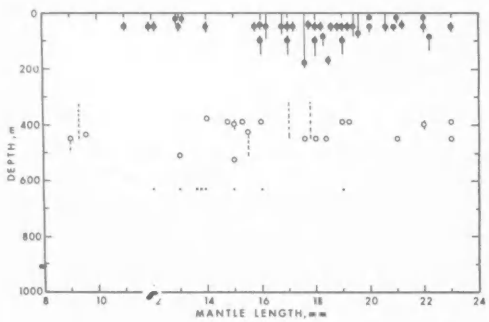

FIGURE 4.—Vertical distribution of *Pterygioteuthis giardi*. Symbols as in Figure 1.

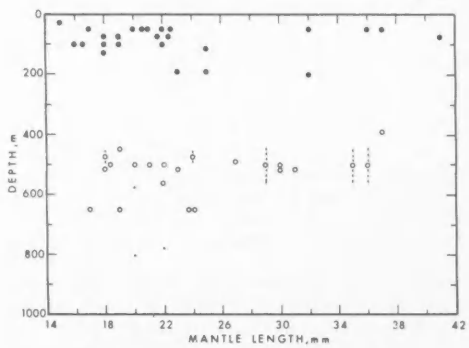

FIGURE 5.—Vertical distribution of *Abralia trigonura*. Symbols as in Figure 1.

Photosensitive Vesicles (Figure 6)

The arrangement of organs is similar to *Abraliopsis* sp. described by Young (1973). Four sets of organs are present; all lie adjacent to the cephalic cartilage. One set is located dorsally, one posteriorly, and two ventrally. Each dorsal organ is situated in a concavity of the cephalic cartilage at the posterodorsal edge of the head. The organ is compact, dorsoventrally flattened and circular to triangular in outline. The posterior organs are located on the posterior surfaces of the optic lobes. Each is approximately elliptical and very flat. The posterior organs have a strong yellow pigment which does not fade after fixation. Other organs contain an orange pigment that is lost after fixation. The posterior organs lie immediately anterior and lateral to the opaque liver and directly anterior to the attachment zone of the transparent head retractor muscles (Figure 6B). The ventral organs on each side consist of two, narrowly joined, flattened lobes. One of these, the anteroventral lobe, is located somewhat anterior and medial to the other. The anteroventral lobe has its medial and anterior ends in a deep depression of the cephalic cartilage. The anteromedial edge of each lobe nearly makes contact with its counterpart of the opposite side. The more posterior of the two lobes, the midventral lobe, lies between the ventral surface of the optic lobe and the cephalic cartilage.

Circular windows, similar to those described in *Abraliopsis* sp. (Young 1973), and characterized by a reduced number of chromatophores, are present above each dorsal organ. A large ventral window, totally lacking chromatophores, lies on the ventral surface of the head above the funnel and below the ventral vesicles.

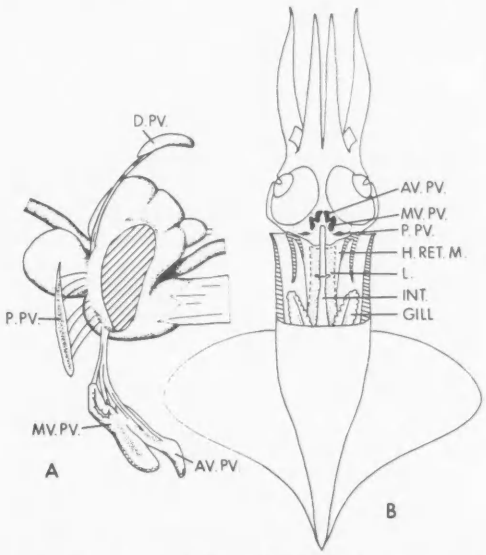

FIGURE 6.—A. Photosensitive vesicles of *Abralia trigonura*. B. Ventral view of *A. trigonura* with portion of mantle removed. This illustration shows the relationship between the posterior photosensitive vesicles, the opaque liver (L), and the mantle cavity. Abbreviations as in Figure 2.

Abralia astrosticta Berry 1909

Vertical Distribution

No specimens were captured during the present program. However, one specimen was taken in a gill net set overnight by T. Clarke on the bottom in 180 m. The National Marine Fisheries Service, NOAA, has captured 44 juveniles (7-38 mm ML (Mantle length)) in pelagic trawls between 10 and 130 m at night and 10 adults in a benthic shrimp trawl at 110 m at night near Hawaii. The type was captured in a bottom dredge between 354 and 650 m, presumably during the day. Roper and Young (1975) indicated that this animal lives near the ocean floor even when migrating.

Photosensitive Vesicles

The organs and associated windows are basically the same as in *A. trigonura*.

Abraliopsis sp. A

Vertical Distribution (Figure 7)

Sixty-seven specimens were captured. Exclud-

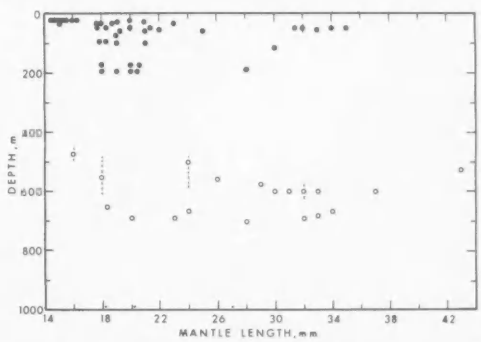

FIGURE 7.—Vertical distribution of *Abraliopsis* sp. A. Symbols as in Figure 1.

ing presumed contaminants, specimens captured during the day came from depths of about 475 to 700 m; 80% were taken between 550 and 700 m. At night, captures were made between about 20 and 200 m; nearly 80% were taken in the upper 100 m.

Photosensitive Vesicles

The organs and associated windows have been described in detail by Young (1973); they are similar to those of *Abralia trigonura*.

Abraliopsis sp. B

Vertical Distribution (Figure 8)

During the day, 23 specimens taken by the Tucker trawl indicate a depth range of 500 to 650 m; most captures came from 500 to 600 m. IKMT data lumped into 100-m increments indicate most specimens came from 400 to 700 m.

At night, 19 specimens from the Tucker trawl probably came from depths between 50 and 100 m. IKMT data lumped into 50-m increments show a strong peak in the 50- to 100-m interval. A few IKMT captures were made as shallow as 15 m.

Photosensitive Vesicles (Figure 2B)

The dorsal and anteroventral organs are similar to other species of *Abraliopsis* and *Abralia*. The posterior lobes, however, are absent, and the midventral lobes are enlarged and extended dorsally. In addition, a thin string of vesicles extends from each midventral lobe dorsally between the brain and the optic lobe to join with the dorsal lobe. The structure of this string is slightly variable, and in some specimens the vesicles found about at midbrain level are slightly enlarged and elongate (Figure 2B). The yellow pigment characteristic of the posterior lobes in related species does not occur in any of the lobes of this species.

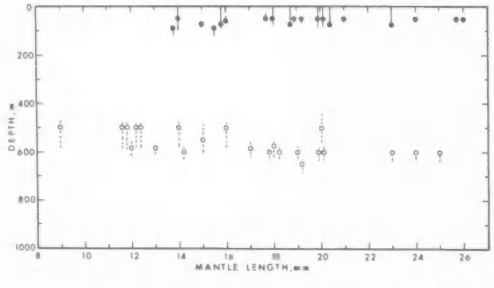

FIGURE 8.—Vertical distribution of *Abraliopsis* sp. B. Symbols as in Figure 1.

Abraliopsis sp. C

Vertical Distribution (Figure 9A)

Only 12 specimens were captured. During the day, five specimens were taken between 500 and 600 m. At night, all of the captures were made in the upper 100m.

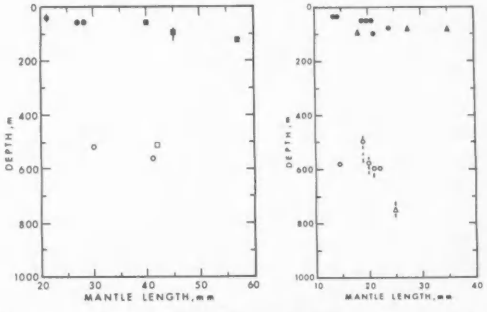

FIGURE 9.—A. Vertical distribution of *Enoploteuthis* sp. A (circles) and *Enoploteuthis* sp. B (squares). B. Vertical distribution of *Abraliopsis* sp. C (circles) and *Thelidioteuthis allesandrinii* (triangles). Symbols as in Figure 1.

Photosensitive Vesicles

The organs are similar to *Abralia trigonura* and *Abraliopsis* sp. A except that the posterior lobe is smaller, slightly more medially located, and continuous with the midventral organ. This latter connection, however, does not have the yellow pigment that the posterior organ possesses. Also, a few scattered vesicles lie on the posterior margin of the nerve from the dorsal organ.

Enoploteuthis sp. A

Vertical Distribution (Figure 9B)

During the day, two captures were made between 500 and 600 m; and at night, three captures were made in the upper 100 m.

Photosensitive Vesicles (Figure 10A)

The organs are similar to *Abralia trigonura*

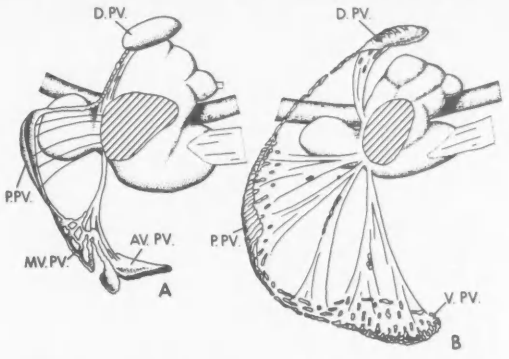

FIGURE 10.—A. Photosensitive vesicles of *Enoploteuthis* sp. A. B. Photosensitive vesicles of *Thelidioteuthis alessandrinii*. Abbreviations as in Figure 2.

with the following exceptions. The midventral organ has a more irregular shape, is less compact, and has a narrow connection with the posterior organ. The posterior organ is continuous with the dorsal organ via a strand of vesicles that extends over the optic lobe. Except for a short segment adjacent to the dorsal organ, this strand contains yellow pigment as does the posterior lobe.

Enoploteuthis sp. B

Vertical Distribution (Figure 9B)

One specimen was captured during the day at 515 m and three were taken at night between 50 and 150 m.

Photosensitive Vesicles

The vesicles are the same as those of *Enoploteuthis* sp. A except for some differences in the posterior organ. The posterior organ in *Enoploteuthis* sp. B is more elongate, more medially located on the optic lobe, and lacks yellow pigment.

Thelidioteuthis alesandrinii (Vérany 1851)

Vertical Distribution (Figure 9A)

During the day, one specimen was taken in an opening-closing tow between 720 and 780 m. At night, three specimens were taken in open tows between 80 and 100 m.

Photosensitive Vesicles (Figure 10B)

Three sets of organs, dorsal, posterior, and ventral, consist primarily of a loose association of variously shaped, mostly independent vesicles (Young 1977). The organs are broad, flat structures, with the greatest concentration of vesicles along the lateral margins of the organs. The organs lack yellow pigment.

Family Ommastrephidae

Symplectoteuthis oualaniensis (Lesson 1830)

Vertical Distribution

Except for larvae, only one specimen was captured in the midwater trawls. This specimen was taken at night by the IKMT which fished at 100 m. This fast-swimming squid normally avoids our trawls. Members of this species are commonly seen at the surface at night around the night-light and a number have been dipnetted. Little is known, however, of their day distribution, although Young (1975b) had assembled evidence which indicates that they live in the upper few hundred meters but may descend on occasion to great depths.

Photosensitive Vesicles (Figure 11A)

Three sets of organs are present: a dorsal, central, and ventral set. The ventral organ lies within the cephalic cartilage at the posterior end of the head and immediately above the posterolateral portion of the funnel. It consists of a series of flat,

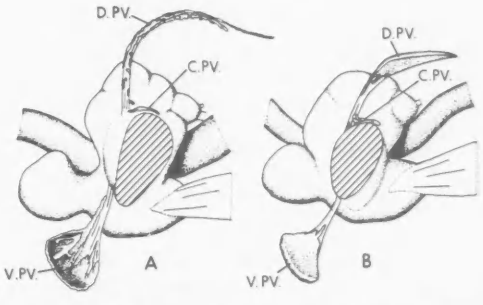

FIGURE 11.—A. Photosensitive vesicles of *Symplecoteuthis oualaniensis*. B. Photosensitive vesicles of *Hyaloteuthis pelagicus*. Abbreviations as in Figure 2.

elongate vesicles that are most numerous at its ventral end. The central organ consists of a few small, flat, elongate vesicles located on the dorsal surface of the optic stalk. The vesicles of the dorsal organ are scattered along a broad arching nerve that extends from the peduncle lobe dorsally then anteriorly along the dorsomedial margin of the optic lobe. The vesicles are flat and irregularly shaped.

Hyaloteuthis pelagicus (Bosc 1802)

Vertical Distribution

The single specimen captured was taken in an opening-closing tow between 1,700 and 2,200 m during the day. The specimen was a gravid female: the ovary was packed with mature eggs, the nidamental and oviducal glands were greatly enlarged, and numerous discharged spermatophores were attached to the lips surrounding the mouth. Specimens in similar condition as well as immature specimens have been captured frequently at a depth of about 100 m at night by the National Marine Fisheries Service, NOAA, in Honolulu using a large Cobb trawl. *Hyaloteuthis pelagicus* typically avoids our midwater trawls. The single day capture demonstrates that this species is capable of descending to great depths. Unfortunately, nothing is known of its normal day habitat.

Photosensitive Vesicles (Figure 11B)

Three sets of organs similar to those of *S. oualaniensis* are present. A small central organ lies just dorsal to the optic stalk and consists of a relatively small number of rather large vesicles. Each dorsal organ lies above the dorsomedial side of the optic lobe and is a large, compact triangular organ with irregularly shaped vesicles. The ventral organ is a flat, compact, oval organ which abuts against the cephalic cartilage above the lateral base of the funnel.

Nototodarus hawaiiensis (Berry 1912)

Vertical Distribution

No specimens have been taken in our midwater trawls; however, 63 specimens were captured in 40-ft shrimp trawls by the National Marine Fisheries Service. Specimens captured during the day came from depths of 230 to 710 m, although only a single capture was made below 420 m. Night captures range from 110 to 410 m. During the late summer and early fall, this species is commonly taken by dip net or near-surface jig at night off the island of Hawaii.

Photosensitive Vesicles (Figure 12A)

Three sets of organs are present similar to those in *S. oualaniensis* and *H. pelagicus*. The central organ is slightly larger than that of *S. oualaniensis* but is positioned similarly. The dorsal organ consists of a flat strip of vesicles that extends from the central organ dorsally to the cephalic cartilage. The margins of this organ are irregular, and thin strings of vesicles extend away from the organ at various places. Where the dorsal organ connects with the central organ, the two can be distinguished by the sizes of their individual vesicles: the small central organ consists of relatively few large vesicles, while the dorsal organ consists of numerous small vesicles. The ventral organ is compact, flattened, and somewhat club-shaped. It occupies about the same position as the corresponding organs in *S. oualaniensis* and *H. pelagicus*.

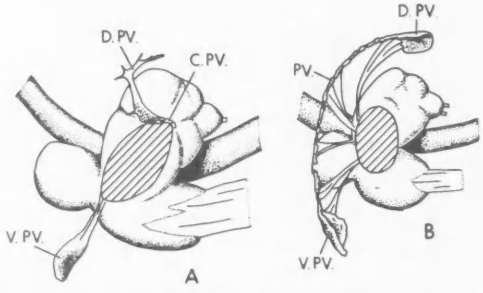

FIGURE 12.—A. Photosensitive vesicles of *Nototodarus hawaiiensis*. B. Photosensitive vesicles of *Histioteuthis dofleini*. Abbreviations as in Figure 2.

Family Histioteuthidae

Histioteuthis dofleini (Pfeffer 1912)

Vertical Distribution (Figure 13)

The vertical distribution of this species has been discussed by Young (1975c). The vertical range is 375 to 850 m during the day; over 80% of the captures came from depths of 500 to 700 m. At

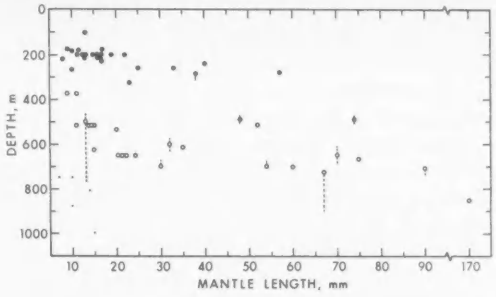

FIGURE 13.—Vertical distribution of *Histioteuthis dofleini*. From Young (1975c). Symbols as in Figure 1.

night, the range is 100 to 500 m; over 85% of the captures came from depths of 150 to 300 m. During both the day and night, larger individuals tend to be found at slightly greater depths.

Photosensitive Vesicles (Figure 12B)

Histioteuthis dofleini has two sets of vesicles, a dorsal and a ventral set, joined by a narrow strand of vesicles. The dorsal and ventral organs are flat and approximately the same size. The dorsal organs lie dorsal to the optic lobes, and the ventral organs lie above the lateral bases of the funnel (R. E. Young 1977).

Histioteuthis celetaria pacifica (Voss 1962)

Vertical Distribution (Figure 14A)

A single day capture came from 550 m. Four night captures came from depths of about 250 to 400 m.

Photosensitive Vesicles

The vesicles are similar to those of *H. dofleini* except that the dorsal and ventral organs are more compact.

Histioteuthis sp.

Vertical Distribution (Figure 14A)

Two day captures came from depths of 575 and 665 m, and four night captures were made between depths of 165 and 275 m.

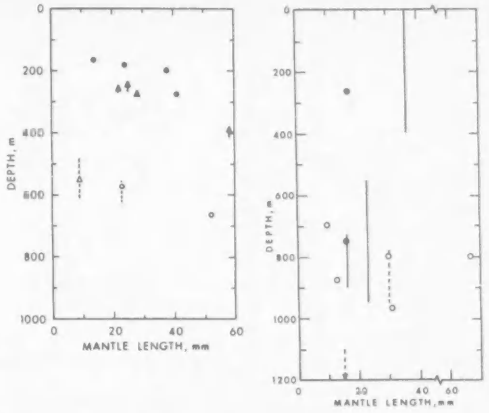

FIGURE 14.—A. Vertical distribution of *Histioteuthis celetaria pacifica* (triangles) and *Histioteuthis* sp. (circles). B. Vertical distribution of *Bathyteuthis abyssicola*. Symbols as in Figure 1.

Photosensitive Vesicles

The vesicles are as in *H. dofleini*.

Neoteuthis sp.

Vertical Distribution

A single small specimen was taken in an IKMT tow that fished between the surface and 350 m at night. Roper and Young (1975) reported nine specimens from the Atlantic Ocean taken in open tows between 1,300 and 2,000 m at night and one specimen taken in a closing net at 900 m at night.

Photosensitive Vesicles (Figure 15A)

Neoteuthis sp. has only one set of organs. Each organ consists of a small grapelike cluster of globular vesicles arising from the medioposterior surface of the peduncle lobe and extending ventrally below the optic stalk.

Bathyteuthis abyssicola Hoyle 1885

Vertical Distribution (Figure 14B)

Five of six specimens captured during the day were taken between 700 and 975 m. The remaining specimen was taken in an oblique IKMT tow that fished between 1,100 and 1,900 m. At night, two specimens were taken in the upper 400 m, a

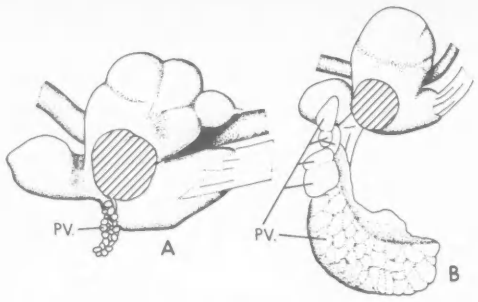

FIGURE 15.—A. Photosensitive vesicles of *Neoteuthis* sp. B. Photosensitive vesicles of *Bathyteuthis abyssicola*. Abbreviations as in Figure 2.

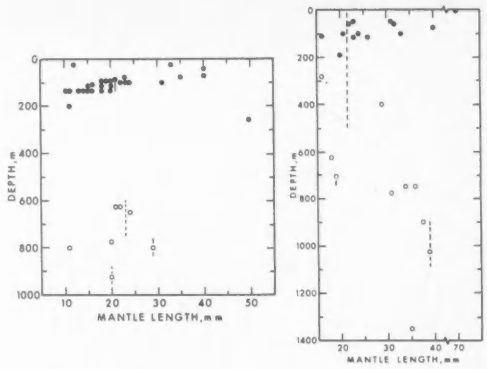

FIGURE 16.—A. Vertical distribution of *Ctenopteryx siculus*. B. Vertical distribution of *Onychoteuthis compacta*. Symbols as in Figure 1.

third was taken in an opening-closing tow at about 750 m, and the fourth in an open oblique tow that fished between 550 and 950 m.

Photosensitive Vesicles (Figure 15B)

The organs have been described in detail by Young (1972a). One set of very large organs is present. Each organ is located adjacent to the posteroventral surface of the eye and above the posterolateral edge of the funnel. Posterior to the organ the skin is only lightly pigmented and forms a "window."

Family Ctenopterygiidae

Ctenopteryx siculus (Vérany 1851)

Vertical Distribution (Figure 16A)

Seven of eight specimens captured during the day came from depths of about 625 to 800 m; the other specimen came from about 925 m. At night 28 specimens were captured between depths of 25 to 260 m; over 80% of the specimens were taken between 50 and 150 m.

Photosensitive Vesicles (Figure 17A)

Ctenopteryx sicula has a single pair of large and highly organized organs. Each organ consists of a single elongate and flattened but curved vesicle. Each organ extends from the posterior end of the supraesophageal mass, beneath the optic stalk, and anterior to the middle subesophageal mass where it joins with its counterpart from the opposite side. The organ, therefore, occupies a groove between the central brain and the optic lobes. The area where the two vesicles join lies just above the funnel approximately at the point where the funnel adductor muscles (bridles) attach to the cephalic cartilage. An iridophore sheath is continuous and encloses both organs in this region, but the vesicles do not actually fuse. That is, the lumen of each vesicle remains separate. The vesicles broaden slightly at their dorsal end and in the region of the junction. The anterodorsal walls of each vesicle are convex and lined with dense layers of iridophores; light enters through the

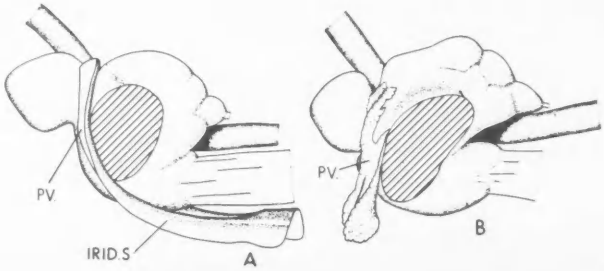

FIGURE 17.—A. Photosensitive vesicles of *Ctenopteryx siculus*. B. Photosensitive vesicles of *Onychoteuthis compacta*. IRID. S.—Iridophore screen. Otherwise, abbreviations as in Figure 2.

posteroventral surfaces. The sensory processes within the vesicles are highly organized, particularly in the ventral portions. The wall of the organ is not particularly thick, and usually has two irregular layers of sensory-cell bodies. The sensory processes arise from all sides of the vesicles; they are straight, parallel, and fill the lumen in the ventral parts of the organ. The sensory processes are about 30 to 50 μm long and lack a detectable core. The dorsal end of the organ lacks the iridophore sheath and has a slightly convoluted wall; the sensory processes are somewhat more widely spaced and do not fill the lumen of the vesicle.

Family Onychoteuthidae

Onychoteuthis compacta (Berry 1913)

Vertical Distribution (Figure 16B)

Twenty-five specimens were captured. Eleven specimens taken during the day came from depths of 240 to 1,350 m. At night, 12 of 14 captures were made between the surface (dip net) and 115 m. The two remaining captures came from depths of 190 and 310 m.

Photosensitive Vesicles (Figure 17B)

Onychoteuthis compacta has a single set of organs. Each organ consists of a large number of small, tightly packed vesicles. Each organ is located on the posterior edge of the optic stalk and extends ventrally and slightly laterally below the central brain along the medial side of the optic lobe. The ventrolateral portion of the vesicle lies directly posterior to the side of the liver and just medial to the head retractor muscles and immediately above the funnel.

Family Octopoteuthidae

Octopoteuthis nielseni Robson 1948

Vertical Distribution (Figure 18A)

Three specimens captured during the day came from depths of about 650 to 765 m. The six night captures came from depths between 100 and 200 m.

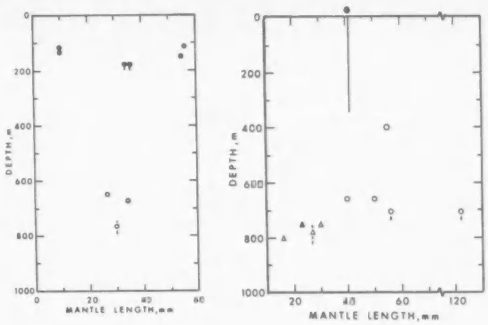

FIGURE 18.—A. Vertical distribution of *Octopoteuthis nielseni*. B. Vertical distribution of *Cycloteuthis serventyi* (triangles) and *Discoteuthis laciniosa* (circles). Symbols as in Figure 1.

Photosensitive Vesicles (Figure 19A)

Two sets of organs are present. A compact ventral organ lies embedded in the thick cephalic cartilage at the anterolateral edge of the statocyst and just medial to the insertion of the head retractor muscles. This organ consists of large, globular, independent vesicles tightly packed together. A series of narrow, very elongate vesicles lie along the nerves from the organ. The central organ lies on the posterior surface of the optic stalk adjacent to the peduncle complex. This large and rather irregularly shaped organ consists of numerous small vesicles.

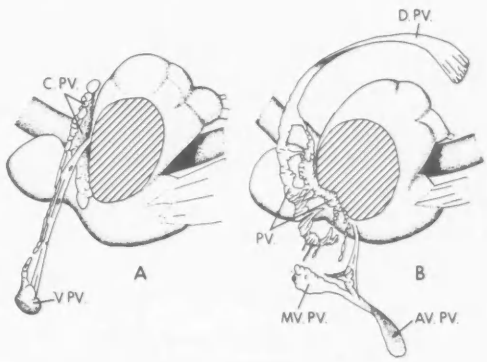

FIGURE 19.—A. Photosensitive vesicles of *Octopoteuthis nielseni*. Photosensitive vesicles of *Cycloteuthis serventyi*. Abbreviations as in Figure 2.

Family Cycloteuthidae

Cycloteuthis serventyi Joubin 1919

Vertical Distribution (Figure 18B)

Three specimens were taken between 750 and 800 m during the day. The single night capture came from an IKMT that fished at 750 m; however, the specimen may be a contaminant, as Roper and Young (1975) listed most of the known night captures of this species from the Atlantic in the upper 200 m.

Photosensitive Vesicles (Figure 19B)

The arrangement of vesicles is complex. On each side of the head, two flattened lobes are located ventral and lateral to the central brain in approximately the positions of the anteroventral and midventral lobes of the *Abraliinae*. The midventral lobe sometimes connects to a complex series of vesicles extending dorsally. These latter vesicles consist of two series: a more posterior series of irregular flattened vesicles lying on the posteromedial surface of the optic lobe; and a thicker, irregular, and rather extensive series of vesicles lying between the optic lobe and peduncle complex. These two series interconnect at various points. At about the level of the optic gland, a thin dorsal organ extends up the medial wall of each optic lobe and onto its anterodorsal surface. This terminal portion gradually widens but remains thin.

Discoteuthis laciniosa Young and Roper 1969

Vertical Distribution (Figure 18B)

Five specimens were taken during the day between 400 and 700 m, although the shallowest capture came from a tow that dipped briefly to 480 m. At night, a single specimen was taken in an oblique tow from the surface to 350 m.

Photosensitive Vesicles (Figure 20A)

The arrangement of vesicles is complex. A broad, flat, irregular ventral lobe is located between the posteroventral surface of the optic lobe and the cephalic cartilage, and opposite the insertion of the head retractor muscles. The broad, flat nerve passing to this lobe bears a series of often isolated vesicles or irregular strands of vesicles which, nearer the brain, join a single, somewhat flattened cord. This central organ extends dorsally and expands somewhat near the optic gland. Although this general pattern holds between specimens, considerable variation in the size of various parts of the central organ occurs.

Family Brachioteuthidae

Brachioteuthis sp.

Vertical Distribution (Figure 21)

Three specimens were captured during the day between 800 and 975 m. Only the mantle of a fourth specimen was present in a day tow at 450 m. The previous tow fished at 900 m and captured one of the other three specimens; the shallow capture is probably a contaminant. Seven of the eight specimens captured at night were taken between 30 and 235 m. The remaining specimen was taken at 1,125 m in an open tow and was a gravid female with sperm masses embedded in the buccal membrane.

Photosensitive Vesicles (Figure 20B)

A single set of organs is present. Each organ is situated on the posterior margin of the optic stalk

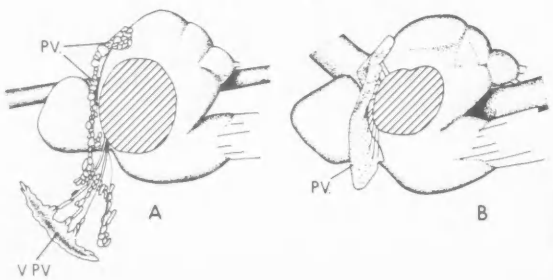

FIGURE 20.—A. Photosensitive vesicles of *Discoteuthis laciniosa*. B. Photosensitive vesicles of *Brachioteuthis* sp. Abbreviations as in Figure 2.

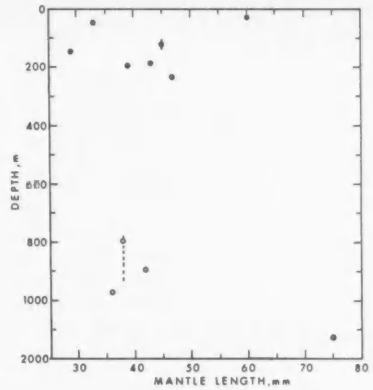

FIGURE 21.—Vertical distribution of *Brachioteuthis* sp. Symbols as in Figure 1.

and extends from the optic gland ventrally and laterally to the level of the ventral surface of the central brain. Each organ consists of numerous small tightly packed vesicles.

Family Chiroteuthidae

Chiroteuthis sp.

Vertical Distribution (Figure 22A)

Three specimens captured during the day were taken between 700 and 800 m. At night, eight specimens were captured between 15 and 750 m; however, six of these came from the upper 200 m.

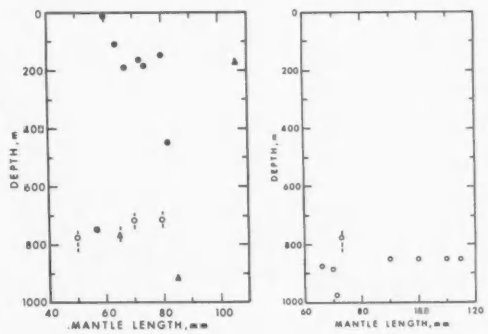

FIGURE 22.—A. Vertical distribution of *Chiroteuthis* sp. (circles) and *Chiroteuthis picteti* (triangles). B. Vertical distribution of Chiroteuthidae gen. sp. Symbols as in Figure 1.

Photosensitive Vesicles (Figure 23A)

One set of small organs is present. Each organ arises on the posterior margin of the optic stalk and extends from the optic gland ventrally to about the level of the ventral surface of the central brain. The organ consists of many small, tightly packed vesicles. Growth of the vesicles from the juvenile stage on is allometric. While the size of each organ increases slightly, the number of component vesicles decreases.

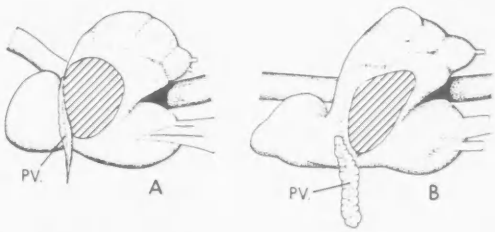

FIGURE 23.—A. Photosensitive vesicles of *Chiroteuthis* sp. B. Photosensitive vesicles of Chiroteuthidae gen. sp. Abbreviations as in Figure 2.

Chiroteuthis picteti Joubin 1894

Vertical distribution (Figure 22A)

Two day captures were made between 750 and 950 m, and a single night capture was made at 175 m.

Photosensitive Vesicles

The organs are essentially the same as in large specimens of *Chiroteuthis* sp. A.

Chiroteuthidae Gen. Sp.

Vertical Distribution (Figure 22B)

All eight specimens of this species were captured during the day between 775 and 975 m.

Photosensitive Vesicles (Figure 23B)

The organs are very similar to those in *Chiroteuthis* spp. One set is present. Each organ consists of small circular vesicles tightly packed into a well-defined organ that attaches to the posteroventral margin of the optic stalk.

Planktoteuthis lippula (Chun 1908)

Vertical Distribution (Figure 24)

Eighteen specimens were captured. Two captures between 200 and 300 m are young animals that probably had not descended to the adult depths. With the exception of a night capture at about 625 m, the remaining animals all came from depths of over 700 m. Among these deeper captures, there is an indication of ontogenetic descent. The largest specimens were captured in an oblique IKMT tow between 1,100 and 1,900 m.

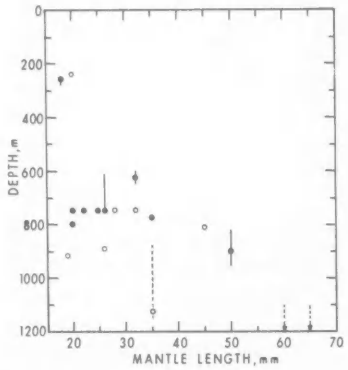

FIGURE 24.—Vertical distribution of *Planktoteuthis lippula*. Symbols as in Figure 1.

Photosensitive Vesicles (Figure 25A)

One set of small organs is present. Each organ is attached to the ventral edge of the optic stalk and consists of a few globular vesicles.

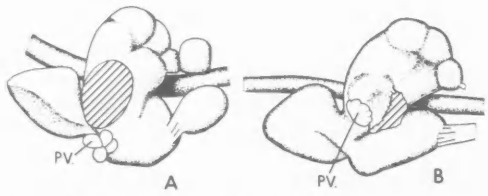

FIGURE 25.—A. Photosensitive vesicles of *Planktoteuthis lippula*. B. Photosensitive vesicles of *Grimalditeuthis bomplandi*. Abbreviations as in Figure 2.

Grimalditeuthis bomplandi (Vérany 1837)

Vertical Distribution (Figure 26A)

Three small specimens were taken at night in the upper 350 m and probably are individuals that had not descended from the larval depths. The larger specimens were all captured during the day between 750 and 1,275 m. The two largest specimens were the two deepest captures.

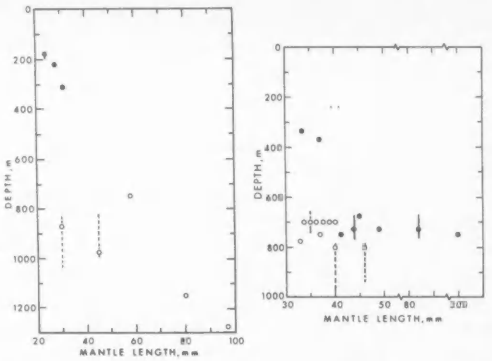

FIGURE 26.—A. Vertical distribution of *Grimalditeuthis bomplandi*. B. Vertical distribution of *Mastigoteuthis famelica*. Symbols as in Figure 1.

Photosensitive Vesicles (Figure 25B)

One set of organs is present. Each organ consists of a small circular cluster of vesicles attached to the posteroventral margin of the optic stalk.

Family Mastigoteuthidae

Mastigoteuthis famelica (Berry 1909)

Vertical Distribution (Figure 26B)

Excluding contaminants, 16 of 18 specimens were taken between 675 and 800 m, both day and night. In addition, three specimens were probably contaminants. Two of these are assigned to a trawl that fished at 240 m during the day. These were probably captured during the previous tow at 700 m, which contained three specimens. Two shallow night captures of small animals may indicate that some of the population moves upward at night. However, since specimens of 41 mm ML or less are not far past the larval condition, these two specimens may represent animals in transit from the larval habitat.

Photosensitive Vesicles (Figure 27A)

Mastigoteuthis famelica has two sets of organs.

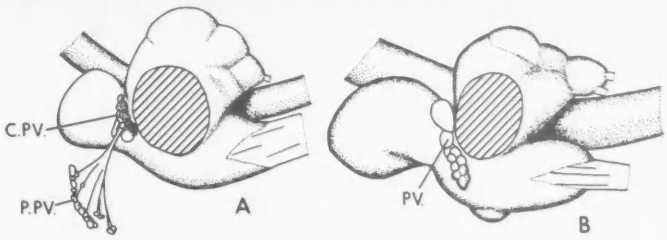

FIGURE 27.—A. Photosensitive vesicles of *Mastigoteuthis famelica*. B. Photosensitive vesicles of *Joubiniteuthis portieri*. Abbreviations as in Figure 2.

The central organs are located on the posterior margin of the optic stalk and consist of a dozen or so independent spherical vesicles. The posterior organs lie on the posterolateral surfaces of the optic lobes opposite the lateral attachment of the head retractor muscles. Each organ consists of a string of several layers of circular or oval vesicles. A few scattered vesicles occasionally occur along the nerves passing from the posterior organ.

Mastigoteuthis inermis Rancurel 1972

Vertical Distribution (Figure 28)

Fifteen specimens were captured during the day at depths of 675 to 870 m; most came from depths of about 700 to 800 m. Ten specimens captured at night came from depths of 255 to 725 m with most specimens being taken between 250 and 450 m.

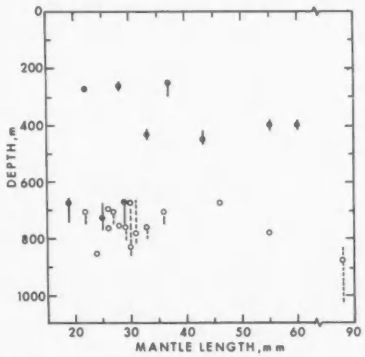

FIGURE 28.—Vertical distribution of *Mastigoteuthis inermis*. Symbols as in Figure 1.

Photosensitive Vesicles

The organs are similar to *M. familica* except that the central organ is flatter and broadly continuous with the posterior organ. The posterior organ extends slightly beyond the insertion of the head retractor muscles and is less elongate.

Family Joubiniteuthidae

Joubiniteuthis portieri (Joubin 1912)

Vertical Distribution

Three specimens, all taken at night, were captured. One (42 mm ML excluding tail) was taken in an oblique tow between the surface and 425 m. A second specimen (64 mm ML) was taken in an opening-closing tow that fished between 480 and 550 m, and a third (85 mm ML) was taken in an open tow that fished at 1,125 m. Roper and Young (1975) listed the two known day captures of this species from the Atlantic Ocean as 800 to 900 m and 2,500 m.

Photosensitive Vesicles (Figure 27B)

One set of small organs is present. Each organ consists of a small number of globular vesicles that form a compact organ. Each organ is attached to the posteroventral margin of the optic stalk.

Family Cranchiidae

Liocranchia valdiviae (Chun 1906)

Vertical Distribution (Figure 29)

Both larvae and adults captured by the Tucker trawl are plotted. IKMT captures have been added where data are weak: specimens >24 mm ML and all specimens captured above 600 m during the day. One hundred fourteen specimens are plotted. Although only a few shallow day captures were made, the vertical distribution pattern is clear: animals between 5 and 15 mm ML predominate in

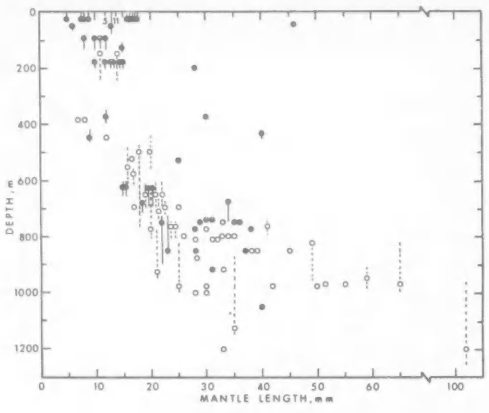

FIGURE 29.—Vertical distribution of *Liocranchia valdiviae*. Symbols as in Figure 1.

the upper few hundred meters. Descent to adult depths begins within the 5- to 15-mm ML size range or occasionally larger. Most specimens 15 to 25 mm ML are captured between depths of 500 and 700 m, while most animals ≥25 mm ML are found deeper than 700 m with progressively larger specimens found at progressively greater depths. Diel vertical migration does not occur. Five large specimens captured at depths of 40 to 525 m at night, however, indicate that some specimens occasionally wander into the upper depths at night. Mature specimens were not captured.

Photosensitive Vesicles (Figure 30A)

Liocranchia valdiviae has a single set of small organs. Each organ is elongate and extends along the posterior side of the optic stalk. Each organ usually consists of three elongated vesicles. A strip of dark brown screening pigment with irregular margins extends along much of the anteromedial edge of the ventral half of the organ. The broad dorsal vesicle either lacks screening pigment or has only a trace of it. The slender middle vesicle has a narrow, often discontinuous strip of pigment which widens ventrally. The ventral vesicle, which is the largest, has a broad, continuous layer of screening pigment.

The vesicles of *L. valdiviae* grow allometrically. At 30 mm ML the vesicles are small, and screening pigment consists of a single small patch on the ventral vesicle. In the largest specimen (102 mm ML), the pigment screen is very extensive and covers much of the anterior surface of the dorsal as well as ventral portions of each organ. The dorsal and ventral vesicles in each organ are somewhat broader in this specimen, making the organ more dumbbell shaped.

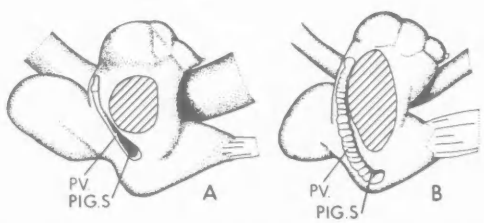

FIGURE 30.—A. Photosensitive vesicles of *Liocranchia valdiviae*. B. Photosensitive vesicles of *L. reinhardti*. Abbreviations as in Figure 2.

Liocranchia reinhardti (Steenstrup 1856)

Vertical Distribution (Figure 31)

All 12 juvenile specimens were captured at night. Ten of the 12 specimens were taken in the upper 100 m; the other 2 came from 150 to 200 m. A single mature specimen was captured at 775 m in a Tucker trawl that failed to close on retrieval. This specimen was a female that had recently spawned: remnants of what appeared to be sperm reservoirs were attached to the inner right wall of the mantle near the base of the funnel; the nidamental glands were gelatinous and extremely swollen; the ovary was depleted; and the muscular tissue of the mantle, fins, head, and arms was flaccid.

Unfortunately, there are no data on the day distribution of this species in Hawaiian waters.

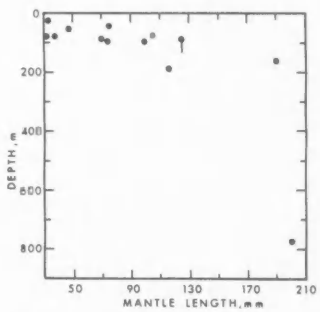

FIGURE 31.—Vertical distribution of *Liocranchia reinhardti*. Symbols as in Figure 1.

However, in the tropical North Atlantic, two specimens of *L. reinhardti* (44 and 48 mm ML) were captured during the day in opening-closing tows between 510 and 600 m, while a 75-mm ML specimen was taken in an open tow that fished between 390 and 800 m (C.C. Lu pers. commun.). Also, M. Clarke (1969) reported specimens of 46 and 69 mm ML from depths between 450 and 810 m during the day in the Atlantic.

Photosensitive Vesicles (Figure 30B)

The organs of *L. reinhardti* have been described by Messenger (1967a). This species has a single large set of organs lying along the posteromedial surface of the peduncle lobe. Each organ consists of a linear array of 20 to 25 tightly packed vesicles. The vesicles are elongated in a transverse direction except for those at the dorsal and ventral ends which are nearly circular. The vesicles are separated from one another by a heavy brown pigment screen which also covers most of the convex anterior side of the organ. Most vesicles within each organ thus form elongate cups which presumably admit light only from one surface. The dorsal vesicle, however, lacks screening pigment from the posterior lateral and dorsolateral surfaces. The ventral vesicle is larger, with photosensitive processes twice as long as those of the dorsal vesicle. It lacks pigment on its ventral and anterior surface. The curvature of the organ and the arrangement of screening pigment allows light to enter different vesicles from a wide range of angles.

Specimens ≤47 mm ML have no screening pigment on the vesicles while those ≥70 mm ML exhibit pigment as described above. The vesicles in the largest specimen (spent female) are slightly larger (especially the ventral vesicle) relative to the brain size than in smaller specimens.

Leachia pacifica (Issel 1908)

Vertical Distribution (Figure 32)

The vertical distribution of *L. pacifica* has been described elsewhere (Young 1975a). This species reaches about 80% of its maximum length in near-surface waters. Large specimens (45-60 mm ML) are found throughout the water column between 30 and at least 1,800 m with those taken from progressively deeper water exhibiting progressively greater sexual maturity. Gravid females were taken at depths >1,300 m.

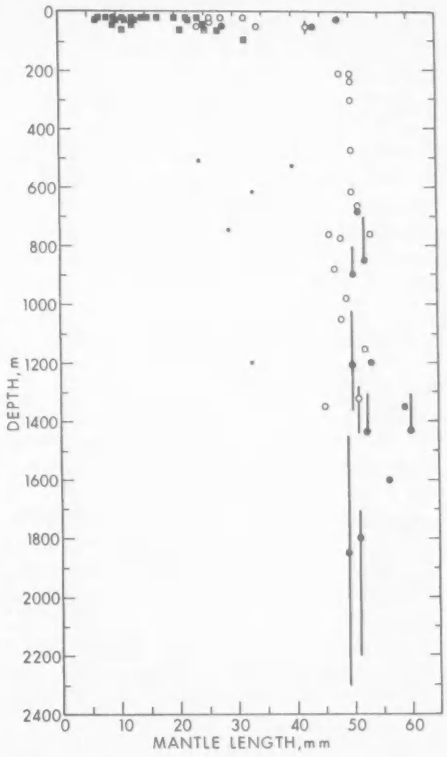

FIGURE 32.—Vertical distribution of *Leachia pacifica*. From Young (1975a). Symbols as in Figure 1.

Photosensitive Vesicles (Figure 33A)

Leachia pacifica has a single set of organs located on the posteroventral surface of the peduncle lobe. Each organ consists of 4 or 5 cup-shaped vesicles that are closely packed into a small oval organ. A dark brown screening pigment covers

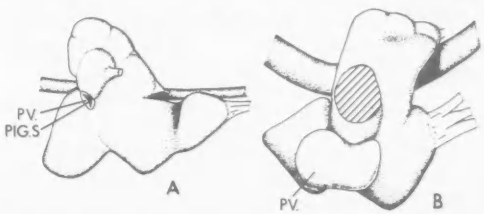

FIGURE 33.—A. Photosensitive vesicles of *Leachia pacifica*. B. Photosensitive vesicles of *Sandalops melancholicus*. Abbreviations as in Figure 2.

much of the anterior and slightly dorsal surface of each organ. This pigment is also found in the walls between some vesicles, tending to isolate them from one another. Although the vesicles are minute in the larva and very small in the adults, a small positive allometric growth of the vesicles seems to occur. Screening pigment first appears on the vesicles between about 20 and 30 mm ML. In the adult, the screening pigment is most extensive and covers the entire anteromedial surface of the organ.

Phasmatopsis fisheri (Berry 1909)

Vertical Distribution (Figure 34)

Over 300 specimens of *P. fisheri* were captured but most were larvae. Metamorphosis occurs at a size of 40 to 50 mm ML.

During the day, six larvae were captured between 150 and 250 m. Seventeen juvenile and adult specimens were captured between about 625 and 800 m; most captures were made between 650 and 775 m.

At night, larvae ≤30 mm ML were taken primarily in the upper 50 m; larvae 31 to 40 mm ML were found throughout the upper 200 m. Fourteen juveniles and adults were taken at night between 90 and 225 m; most captures were made between 100 and 200 m.

Photosensitive Vesicles (Figure 35)

Phasmatopsis fisheri has a single set of large organs. Each organ consists of a broad, elongate vesicle that extends from the optic gland on the dorsal surface of the optic stalk ventrally over the posterior surface of the peduncle complex onto the side of the ventral subesophageal mass, where it bends slightly dorsally. Each organ is thick laterally and medially. Most of the anterior, medial, and lateral surfaces of each organ are covered by dark brown pigment screen. The dorsal tip of each organ lacks screening pigment on its lateral portion and has limited pigment screen on its medial portion. The curvature of each organ allows light to enter various parts from a wide range of angles.

The anterior wall of each organ consists of little more than a membrane backed by dense pigment. The posterior wall and the walls of the dorsal and ventral ends of each organ contain 4 or 5 layers of sensory-cell bodies. Sensory processes are longer (215 μm) and thinner (inner diameter 2 to 4 μm) in the ventral parts of the organ than in the dorsal

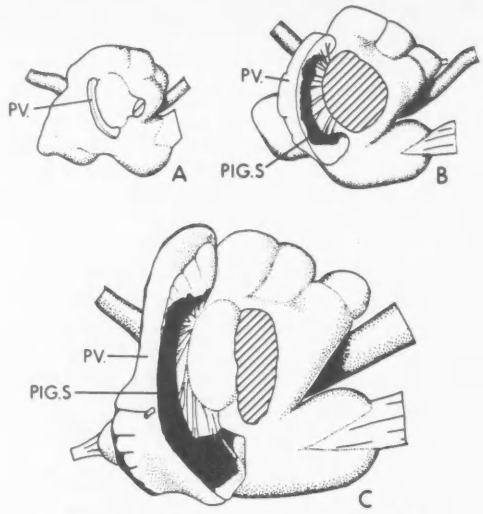

FIGURE 35.—Photosensitive vesicles of *Phasmatopsis fisheri*. A. Larva, 35 mm ML. B. Juvenile, 70 mm ML. C. Adult, 130 mm ML. Abbreviations as in Figure 2.

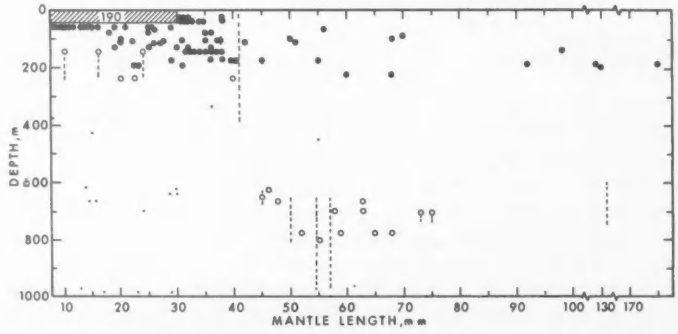

FIGURE 34.—Vertical distribution of *Phasmatopsis fisheri*. Symbols as in Figure 1.

parts (length 155 μm, inner diameter 3 to 6 μm). The processes are long and slender and organized in a straight, parallel alignment.

Each organ is small in larvae and lacks screening pigment. At 35 mm ML, the vesicles form a narrow strip along the posterior surface of the peduncle lobe (Figure 35A). The largest larvae have relatively small organs without screening pigment; the youngest juveniles have large organs that are heavily pigmented. In the juvenile and adult stages, the organ exhibits positive allometric growth (compare Figure 35B and C). In the adult stages, the organ exhibits positive allometric growth (compare Figure 35B and C). In the brain. The ventral half of the organ is particularly enlarged and the organs on each side of the brain contact broadly (but do not fuse) below the ventral midline of the brain.

Taonius pavo (LeSueur 1821)

Vertical Distribution (Figure 36)

The vertical distribution of *T. pavo* has been described by Young (1975d). Larvae probably live in the upper 400 m, although only one capture was made. Juveniles were found primarily between 600 and 650 m, and adults were captured between 725 and 970 m. Diel vertical migration does not occur.

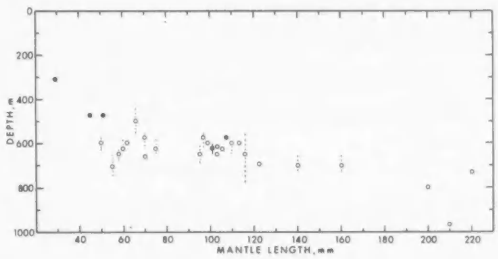

FIGURE 36.—Vertical distribution of *Taonius pavo*. From Young (1975d). Symbols as in Figure 1.

Photosensitive Vesicles (Figure 37)

Taonius pavo has a single set of organs located on the posteroventral side of the peduncle complex. Each organ consists of a single oval vesicle. No screening pigment is present. The large size of the vesicle in a 220-mm ML specimen belies its internal structure. The large central region of the

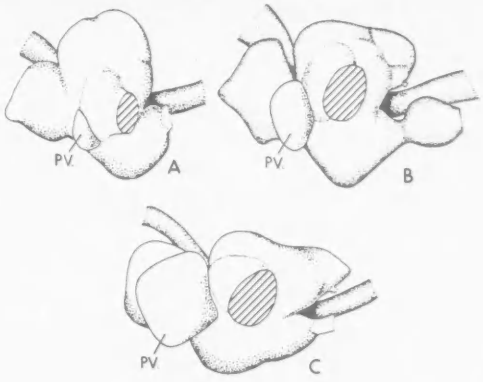

FIGURE 37.—Photosensitive vesicles of *Taonius pavo*. A. Larva. B. Juvenile, 140 mm ML. C. Adult, 220 mm ML.

lumen is unoccupied. Sensory processes occupy about 1/5 (i.e., about 230 μm) of the lumen diameter on the anterior, posterior, and dorsal sides and slightly more (about 300μm) on the ventral sides. The processes are loosely packed and intertwined to a large extent dorsally and more tightly packed ventrally. Inner diameters of the processes vary greatly from about 3 to 30 μm. The wall on the dorsal half of the organ contains about two layers of sensory-cell bodies compared with about three layers ventrally. In a 140-mm ML juvenile, the dissected vesicle was also hollow, with an even thinner region of the lumen occupied by sensory processes. The organs exhibit positive allometric growth (Figure 37).

Sandalops melancholicus Chun 1906

Vertical Distribution (Figure 38)

The vertical distribution in this species has been reported by Young (1975d). Larvae were found in the upper 400 m. Juveniles were captured between 450 and 674 m, and two adults were captured near 800 and 1,075 m. Diel vertical migration does not occur.

Photosensitive Vesicles (Figure 33B)

Sandalops melancholicus has a set of organs located along the ventral surface of the peduncle complex. Each organ consists of a single bilobed vesicle (R. E. Young 1977). Slight positive allometric growth of the vesicles occurs between the juvenile and adult stages.

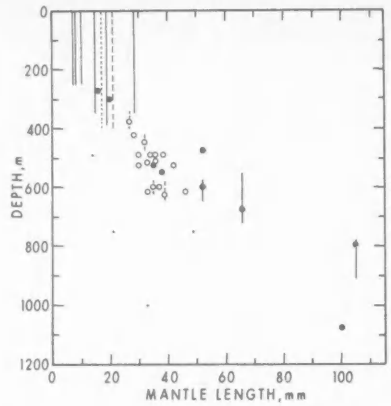

FIGURE 38.—Vertical distribution of *Sandalops melancholicus*. From Young (1975d). Symbols as in Figure 1.

Helicocranchia beebei Robson 1948

Vertical Distribution (Figure 39)

Including larvae, 47 specimens were captured. Although day and night captures are not well intermingled in Figure 39 (due largely to sampling inequities), the data indicate that this species does not migrate. Rather, it seems to undergo ontogenetic descent. The youngest specimens were captured between 100 and 200 m. Progressively larger specimens were generally taken at progressively greater depths, although the relationship of size to depth is not very precise. The deepest capture was probably at 1,200 m. Mature specimens were not captured.

Photosensitive Vesicles (Figure 40A)

One set of organs is present. Each organ consists of a single small oval vesicle located on the posterior surface of the peduncle complex. No screening pigment is present. Very slight, if any, positive allometric increase in the size of the vesicles occurs from juveniles to the largest specimens.

Bathothauma lyromma Chun 1906

Vertical Distribution (Figure 41)

Although only 12 specimens were captured, a general pattern of ontogenetic descent is evident.

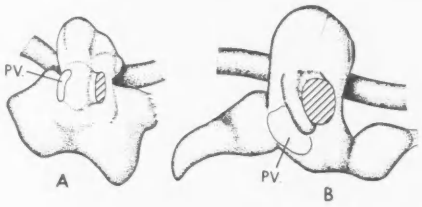

FIGURE 40.—A. Photosensitive vesicles of *Helicocranchia beebei*. B. Photosensitive vesicles of *Bathothauma lyromma*. Abbreviations as in Figure 2.

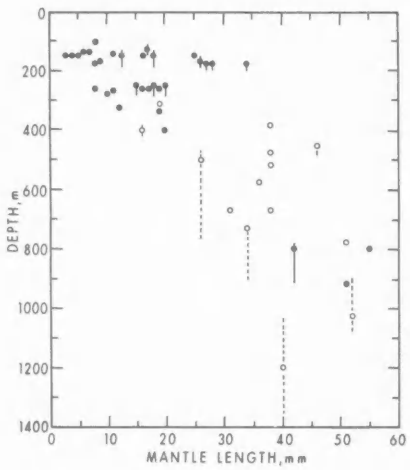

FIGURE 39.—Vertical distribution of *Helicocranchia beebei*. Symbols as in Figure 1.

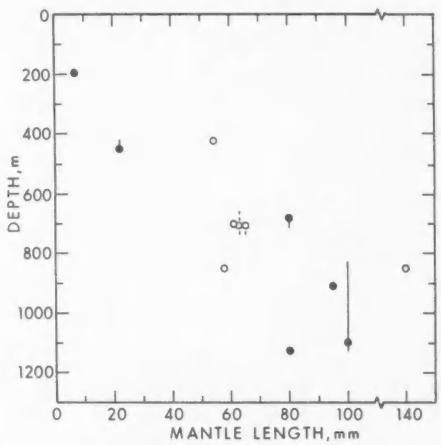

FIGURE 41.—Vertical distribution of *Bathothauma lyromma*. Symbols as in Figure 1.

Day and night captures were in the same depth range, indicating that diel vertical migration does not occur. The three specimens captured at the greatest depths were gravid females. The specimen captured at 910 m had sperm receptacles imbedded in the back of the head and in the anterodorsal surface of the mantle. The nidamental and oviducal glands were greatly enlarged and the entire visceropericardial coelom was packed with large eggs. The muscular tissue was slightly flabby. The specimen captured at 1,125 m exhibited almost identical features. The specimen captured at about 1,100 m had similarly placed sperm reservoirs, less extensively enlarged nidamental and oviducal glands, and lacked eggs (apparently due to damage during capture). This specimen exhibited no sign of muscular degeneration. The mantle cavity of this specimen had two very long arms from another specimen (presumably a male) attached to the inner wall of the mantle. The largest specimen was an immature female. Its size was largely due to its fixation in a relaxed state. In this species, the pen is extraorinarily delicate and accurate measurements of contracted, crumpled specimens are nearly impossible.

Photosensitive Vesicles (Figure 40B)

Bathothauma lyromma has a single set of organs. Each organ consists of a flat oval vesicle located on the posteroventral surface of the peduncle complex. No screening pigment is present. Slight positive allometric growth of the vesicles occurs from juveniles to adults.

Galiteuthis pacifica (Robson 1948)

Vertical Distribution (Figure 42)

The 27 specimens captured indicate a broad vertical range for this species. Fourteen of the 19 captures of specimens >20 mm ML came from depths of 700 m or more. The data indicate that diel vertical migration does not occur.

Photosensitive Vesicles

The vesicles of this species are similar to those of *G. phyllura* described by Young (1972a). A single set of organs is present. Each organ consists of a large oval vesicle attached to the posteroventral surface of the peduncle complex. Considerable positive allometric growth of the vesicles occurs.

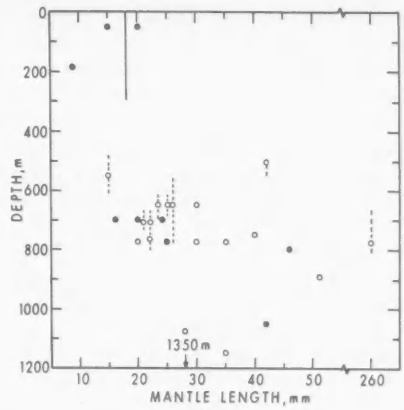

FIGURE 42.—Vertical distribution of *Galiteuthis pacifica*. Symbols as in Figure 1.

Order Octopoda

Family Bolitaenidae

Eledonella pygmaea Verrill 1884

Vertical Distribution (Figure 43)

Eighty specimens were captured. Day and night captures were in the same depth range (except above 300 m where day trawling was minimal), indicating that diel vertical migration does not occur. Most specimens between 5 and 15 mm ML

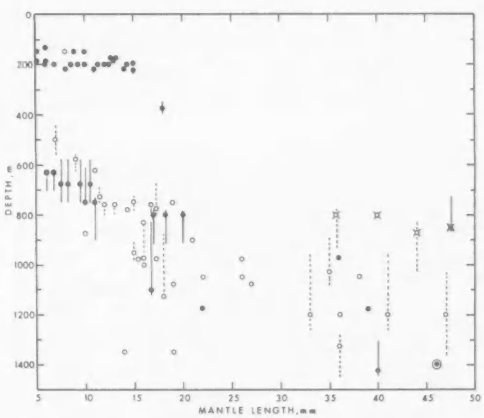

FIGURE 43.—Vertical distribution of *Eledonella pygmaea*. Circles with crosses represent brooding females. Double circle represents a gravid female. Otherwise symbols as in Figure 1.

were captured either around 200 m or below 600 m. Apparently the size at which young begin their descent to adult depths is rather variable. The deep captures exhibit a clear pattern of ontogenetic descent. At 25 mm ML or larger all specimens (excluding brooding females) were captured between depths of 975 and 1,425 m. Four females, apparently brooding, were captured between about 800 and 870 m.

The pigmentation of the female changes as she becomes gravid: the chromatophores over the mantle and especially over the aboral surface of the arms and web become more numerous, and the oral surfaces of the arms and web develop an even denser pigmentation. Nearly all iridophores are lost. At the same time the arms and the web become thicker. The web between the dorsal six arms becomes more extensive, and the web between the two ventral arms is reduced. These dark octopods spawn and apparently brood their young (Young 1972b). Five specimens taken from horizontal tows exhibited this increased pigmentation. In four cases, the ovary was depleted, and in the fifth, captured at 1,400 m, the eggs were not fully mature, but were considerably larger than in an immature female of approximately the same size. In two cases egg strings with developing embryos were found in the same trawl with dark and presumably brooding females.

No mature males were taken. However, judging from the development of the hectocotylus, the penis, and the spermatophore glands, two specimens captured at 1,200 and 1,425 m were nearly mature. Another slightly less mature specimen was taken at 1,325 m. Three still less mature specimens were taken between 1,175 and 1,200 m, while a large male taken at 1,025 m was the least developed of all.

Photosensitive Vesicles (Figure 44A)

The photosensitive vesicles consist of a single pair of organs; each organ is a spherical vesicle attached to the posterior margin of the stellate ganglion.

Japetella diaphana Hoyle 1885

Vertical Distribution (Figure 45)

Seventy-four specimens were captured. Diel vertical migration does not occur. Specimens <20 mm ML were captured mostly in two regions, between 170 and 270 m and between 500 and 800 m,

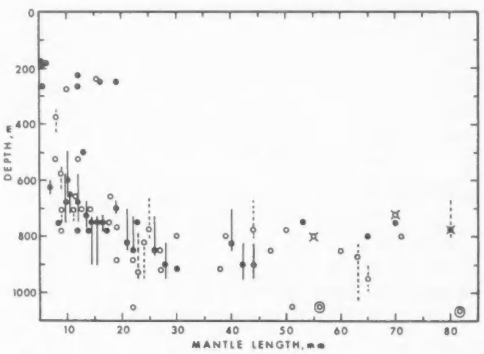

FIGURE 45.—Vertical distribution of *Japetella diaphana*. Circles with crosses represent brooding females. Double circles represent gravid females. Otherwise symbols as in Figure 1.

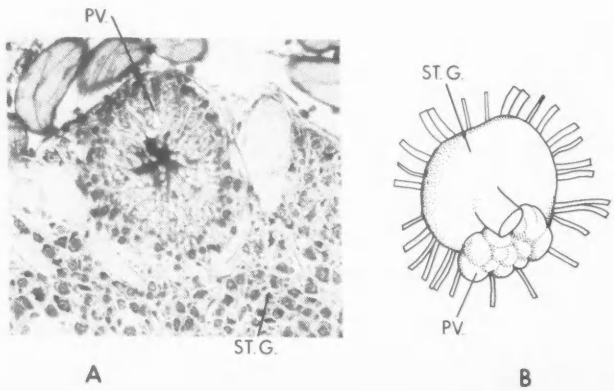

FIGURE 44.—A. Section through the photosensitive vesicle of adult *Eledonella pygmaea*. B. Photosensitive vesicles of *Amphitretus pelagicus*. ST. G.—Stellate ganglion. Otherwise symbols as in Figure 1.

where they exhibited an ontogenetic descent. The depth range for specimens ≥20 mm ML was 725 to 1,065 m; nearly 90% of the animals occur between 700 and 950 m and nearly 60% between 750 and 850 m. Gravid and brooding females were found at the extremes of this range. Two gravid females were captured at 1,050 and 1,065 m while three spent and presumably brooding females were taken between 725 and 800 m. As in *E. pygmaea*, the gravid and spent females have a very heavy pigmentation and lack most of the iridophores present in younger specimens. Five such females were captured in horizontal tows. One gravid female with a sperm mass embedded in the gelatinous tissue between the second and third arms was taken at 1,050 m. Another taken at 1,065 m had been gutted in the trawl but had not spawned: the musculature was firmer than in spent females, and the catch contained a large number of octopod eggs which undoubtedly came from the ruptured ovary. Three specimens taken between 725 and 800 m probably had spawned: two had depleted ovaries and the third was gutted but had deteriorated musculature. In the same tow with the last specimen were four newly hatched larvae, presumably from the brood of the female. One large, heavily pigmented female taken in an oblique tow had the remnants of an egg string dangling from one of the large suckers of the third arm. Two eggs were completely engulfed by the sucker, while a third dangled from the broken egg string extending from the sucker. No mature males were taken.

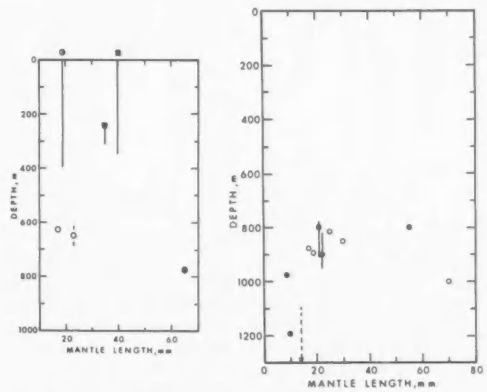

FIGURE 46.—A. Vertical distribution of *Amphitretus pelagicus* (squares) and *Vitreledonella richardi* (circles). B. Vertical distribution of *Vampyroteuthis infernalis*. Half-closed circles represent a twilight capture. Otherwise symbols as in Figure 1.

Photosensitive Vesicles

The vesicles are as in *E. pygmaea*.

Family Amphitretidae

Amphitretus pelagicus Hoyle 1885

Vertical Distribution (Figure 46A)

Two specimens were taken at night in the upper 350 m.

Photosensitive Vesicles (Figure 44B)

Amphitretus pelagicus has one set of organs. They lie on the stellate ganglia immediately anterior to the entry points of the pallial nerves. Each organ consists of a large complex of a dozen or more generally circular vesicles which cover most of the anterior wall of the ganglion.

Family Vitreledonnelidae

Vitreledonnella richardi Joudin 1918

Vertical Distribution (Figure 46A)

Four specimens were captured. One small specimen was taken in an oblique twilight tow between the surface and 400 m. Two other small specimens were taken between 600 and 650 m during the day. One large specimen was captured at 775 m during the night.

Photosensitive Vesicles

An organ consisting of a single spherical vesicle is located on the posterior margin of each stellate ganglion.

Order Vampyromorpha

Family Vampyroteuthidae

Vampyroteuthis infernalis Chun 1903

Vertical Distribution (Figure 46B).

Eleven specimens were captured. Ten of the 11 were taken between depths of 800 and 1,200 m. The remaining specimen came from an open oblique tow that fished between 1,100 and 1,900 m. Diel vertical migration does not occur.

Photosensitive Vesicles

The vesicles have been described in detail by Young (1972a). One set is present. They are located in the dorsal wall of the mantle cavity at the base of the funnel. Each organ consists of a small cluster of spherical vesicles.

Order Sepioidea

Heteroteuthis hawaiiensis (Berry 1909)

Vertical Distribution (Figure 47)

The distribution of this species has been discussed by R. E. Young (1977). During the day, specimens ≤17 mm ML were taken between 250 and 350 m; larger specimens were taken between 375 and 650 m. At night, most specimens <17 mm ML came from depths between 150 and 200 m; larger specimens were taken between depths of 110 and 550 m. Males and females mature at about 15-16 mm ML.

Photosensitive Vesicles (Figure 48)

Two sets of organs are present (R. E. Young 1977). The more dorsal set lies on the posterior margin of the peduncle complex and consists of a short and narrow string of tiny vesicles. An even

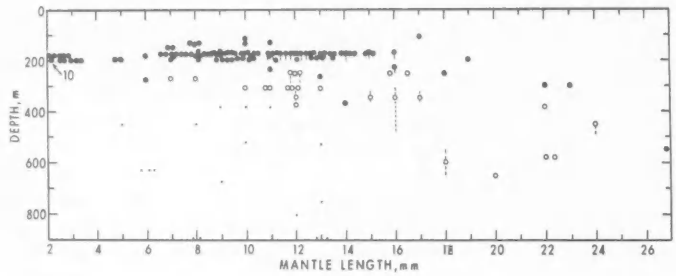

FIGURE 47.—Vertical distribution of *Heteroteuthis hawaiiensis*. From R. E. Young (1977). Symbols as in Figure 1.

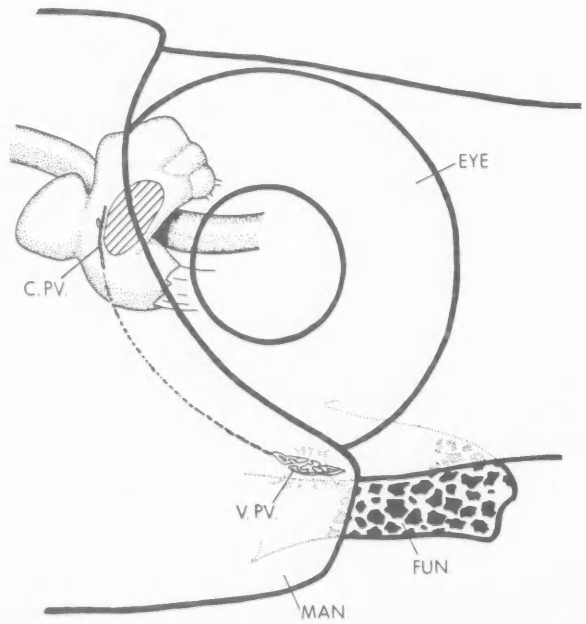

FIGURE 48.—Photosensitive vesicles of *Heteroteuthis hawaiiensis*. In this figure the outline of portions of the head and mantle are superimposed to give a clear perspective of the peculiar arrangement of vesicles in this species. EYE—eye; FUN.—funnel; MAN.—mantle. Otherwise abbreviations as in Figure 2.

narrower string of tiny vesicles extends ventrally around the eyes and joins a rather large but extremely thin, loosely associated group of vesicles that lies over the lateral base of the funnel.

DISCUSSION

Vertical Distribution

The numbers of cephalopod species taken in different 100-m depth zones for the upper 1,400 m showed a broad peak between 500 and 800 m during the day (Figure 49). An abrupt increase in the number of species near 400 m was obscured by the method of analysis: eight species occurred for the first time between depths of 375 and 450 m. To indicate faunal change, the number of species found for the first time in each zone (i.e., depth zones containing species upper range limits) were compared with zones where species found in lesser depths were absent for the first time (i.e., depth zones immediately below the lower range limits) (Figure 49).

The peak at 700-800 m in the summed plot of species added and species lost indicates that many species dropped out in the 600-700 m zone and many were added in the 700-800 m zone. The chart also indicates that only two species were encountered for the first time at 800 m or below. One was the poorly sampled *Brachioteuthis* sp. and the other was deep-living *Vampyroteuthis infernalis*. The data indicate peak species richness in the upper few hundred meters with relatively little change between 300 and 1,000 m during the night (Figure 49).

Numbers of individuals in different depth zones in the upper 1,400 m (exclusive of young individuals, captures in oblique tows, and contaminants) were also examined (Figure 50). During the day, the greatest abundance of individuals occurred between 400 and 700 m. This peak reflects the dominance of the enoploteuthids, especially *Pyroteuthis* and *Pterygioteuthis* spp. The high rate of capture in the 300- to 400-m zone was due in part to a few species whose upper limits extended slightly above 400 m. Nevertheless, an abrupt increase in number occurred in the 400- to 500-m zone. The rates of capture below 1,000 m were unreliable due to the small amount of trawling.

The night data in the upper 400 m were lumped into 50-m increments due to greater control over trawling depths in near-surface waters. The largest catches at night were made in the upper 200 m. In this region two peaks were apparent (Figure 50). The peak in the 50- to 100-m zone was largely due to *Pterygioteuthis microlampas*, the

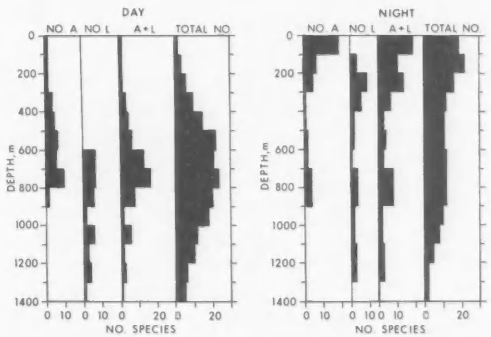

FIGURE 49.—Numbers of species versus depth. The histograms were based on species ranges from midwater trawl data. Data were lumped into 100-m depth increments and were not corrected for unequal trawling times at different depths. Data for some species were very meager. Young stages found in near-surface waters that can be distinguished by an abrupt change in habitat or by a metamorphosis have been eliminated from the figures. No. A—number of species added (i.e., found for the first time in a given depth zone). No. L.—number of species lost (i.e., absent from a given depth zone but present in the shallower zone). A + L—sum of two previous histograms. Total No.—total number of species in each depth zone.

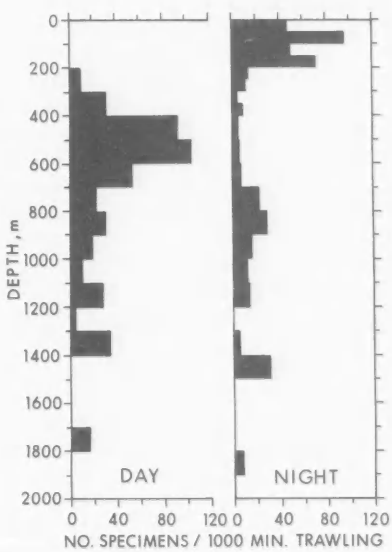

FIGURE 50.—Total catch rate of numbers of cephalopod specimens from both trawls.

most abundant species in the collection. The peak in the 150- to 200-m zone was largely due to *Pyroteuthis addolux* and *Heteroteuthis hawaiiensis*; young *Histioteuthis dofleini* also contributed considerably. Young *Eledonella* were also found in this zone although they were excluded from the figures as "larvae."

The zone between 200 and 700 m was sparsely inhabited at night. The peak between 700 and 1,000 m represented the deep nonmigrating population. The capture rate in this region was almost identical to the day capture rate at the same depths: deep-living migrators were few.

The total rate of capture for the water column during the day was 459 specimens/1,000 min of trawling. Surprisingly, the total capture rate at night was only 309 specimens/1,000 min. This difference was largely due to smaller-than-expected catches at night in the upper 200 m of the few most abundant species. The reason for the low night catches is unknown. Another estimate of the number of animals in the upper 250 m at night was obtained by assuming that the day peak from 300 to 700 m (minus the night catch at these depths) shifted into this upper zone at night (see below). On this basis, nearly 80% of the individuals occurred in the upper 250 m at night. If one considers also the abundant ommastrephids which avoided midwater trawls but occurred in near-surface waters at night, then only a small percent of the total number of individuals would remain below 250 m at night.

In many species, most of the population shifted upward at night. Such day-night differences existed in at least 25 of the 47 species examined, based on present data and literature records. Adequate data were lacking for ommastrephids and *Neoteuthis* sp. Therefore, where the vertical ranges are known, nearly 60% of the species exhibited diel shifts in habitat. Species not exhibiting diel migrations belonged primarily to the Cranchiidae (seven species) and the Octopoda (five species).

At least 18 of the 25 species that exhibited diel migrations occurred almost exclusively in the upper 250 m at night. These included all 11 enoploteuthids, *Liocranchia reinhardti*, *Phasmatopsis fisheri*, *Ctenopteryx siculus*, *Octopoteuthis neilseni*, *Brachioteuthis* sp., *Chiroteuthis* sp., *Onychoteuthis compacta*, and young *Heteroteuthis hawaiiensis*. Two species for which the data were incomplete (*Cycloteuthis serventyi* and *Chiroteuthis picteti*) probably belonged to this category as well. Therefore, at least 80% of the migratory species occurred in the upper 250 m at night.

Amesbury (1975) examined vertical zonation of midwater fishes during the day off Hawaii. He concluded that the water column could be divided into three regions: epipelagic, mesopelagic, and bathypelagic zones. The boundary between the epipelagic and mesopelagic zones occurred at about 400 m and was marked by a sharp increase in the numbers of individuals. This boundary appeared to apply equally well to cephalopods. The boundary between the mesopelagic and bathypelagic zones occurred at about 1,200 m. This boundary was marked by a noticeable decrease in fish numbers and represented the greatest day depths of vertically migrating fish. This lower boundary was not applicable to cephalopods; there was no comparable decrease in numbers of individuals; and this depth seemed to be well below the range of vertical migrators. Amesbury further divided the mesopelagic zone into upper and lower zones with the boundary at about 650 to 700 m. Cephalopods exhibited maximum species turnover at about this depth, as well as changes in light-related adaptations in some species (Young 1975d). Although fish and cephalopod distributions differed with respect to the lower boundary, the distribution of cephalopods generally supported Amesbury's zonation.

In spite of the rather small size of the collection, some evidence of vertical habitat separation among closely related species emerged. Three of the more abundant species belong to the subfamily Pyroteuthinae: *Pyroteuthis addolux*, *Pterygioteuthis microlampas*, and *P. giardi*. In general body proportions and armature, *P. microlampas* was more similar to *Pyroteuthis addolux* than to its congener. During the day, these two species occupied the same depths around 500 m. At night, their populations peaked at distinctly different depths: *Pterygioteuthis microlampas* occurred primarily between 50 and 100 m, while *Pyroteuthis addolux* occurred primarily between 150 and 200 m. Although the data were less clear for *Pterygioteuthis giardi*, this species seemed to center around 400 m during the day and in the upper 100 m at night with about half of the population in the upper 50 m. Thus this species was shallower than its two relatives during the day and tended to be shallower at night, although broad overlap occurred with its congener.

Two species of the genus *Abralia* occurred off Hawaii. *Abralia trigonura* was a common vertical migrator in the area sampled of the open ocean, while *A. astrosticta* was never taken there. *Abralia astrosticta* seems to be a vertical migrator that moves in close proximity to the ocean floor (Roper and Young 1975).

Two species of *Mastigoteuthis* were taken. Both species shared the same day habitat at 700 to 800 m. At night, the population of *M. inermis* spread upward in the water column 400 or 500 m. Although the data were few, *M. famelica* appeared to spread little or not at all.

One of the clearest cases of habitat separation of congeners occurred in *Liocranchia*. *Liocranchia valdiviae* was taken in lower mesopelagic depths during the day and it did not migrate. *Liocranchia reinhardti* was taken in near-surface waters at night and apparently occurred in upper mesopelagic depths during the day.

Although the octopods *Japetella diaphana* and *Eledonella pygmaea* are placed in separate genera, they are very closely related. Both were taken in deep waters and did not migrate. The adults (except brooding females) were taken at distinctly different depths: *E. pygmaea* occupied depths from 975 to 1,425 m while *J. diaphana* occupied depths primarily from 700 to 950 m. Young stages prior to descent were found in near-surface waters. In this habitat *E. pygmaea* was captured primarily at 200 m or just above while *J. diaphana* was captured primarily below 200 m. Young stages of both species in the process of descent occupied depths of about 400 to 800 m or more. The data indicated, however, that at any given size, except for those just beginning descent, the young of *E. pygmaea* occupied greater depths than the young of *J. diaphana*.

In the genus *Abraliopsis* three species were taken: *Abraliopsis* sp. A and *Abraliopsis* sp. C form the most closely related species pair. The available data show no obvious habitat differences. Although the more common *Abraliopsis* sp. A reached a considerably larger size than species C (43 mm ML vs. 33 mm ML), young individuals of species A, however, apparently cooccurred with species C of the same size. The day and night habitats of *Abraliopsis* sp. B were not separable from its two congeners.

Three other groups of congeners were taken (i.e., in *Enoploteuthis*, *Histioteuthis*, and *Chiroteuthis*). No differences in habitats were found within these groups; however, the data were extremely sparse.

Reproduction

Young (1972b) presented evidence for brooding in *Eledonella pygmaea* (incorrectly reported as *Bolitaena microcolyla*) and suggested that brooding occurs in all pelagic octopods. Additional evidence from the present study substantiated the brooding habit for *E. pygmaea*. In addition, evidence indicating brooding in the octopod *Japetella diaphana* was found. This species underwent changes at maturity similar to *E. pygmaea*. Further, newly hatched young have been found in the same trawl with spent females, and in one case the remnants of an egg string was found attached to an arm sucker of such a female.

In both species, gravid or near-gravid females were taken only at the lower limits of the species' vertical range. Although mature males were not taken, those nearest maturity were also taken in the lower parts of the depth range. Apparently, mating takes place at the lower depth limits of the population. Brooding females, on the other hand, were found only at the upper limit of the adult population in *J. diaphana* and only well above the upper limit of the remaining adult population in *E. pygmaea*. The brooding females of both species occurred around 800 m. Presumably the females migrate upward to around 800 m either just before or just after spawning. The increased risk of predation above 800 m probably prevents the female from further upward movement: the numbers of fishes increase greatly above 800 m (Amesbury 1975), and visual detection of the large silhouette presented by a brooding female should be possible above about 750 to 775 m (Young and Roper 1977). The upward movement must be unrelated to feeding since brooding females do not feed (Young 1972b). The upward migration may simply decrease the distance the young must travel after hatching to their larval habitat near 200 m.

A number of cephalopods may spawn at the lower end of their depth range. Evidence for deep-spawning was found in several vertically migrating species. A single spent female of *Liocranchia reinhardti* was captured at 775 m at night, well below its normal night habitat in the upper 200 m. A single gravid, mated female of *Brachioteuthis* sp. was captured at 1,125 m at night; its normal night habitat is in the upper 200 m. *Heteroteuthis hawaiiensis* migrated vertically and exhibited

narrow vertical ranges day and night until sexual maturity was reached; a poorly defined ontogenetic descent then ensued. Unfortunately, no other clues to spawning depth are known.

The nonmigrating species that exhibit a gradual ontogenetic descent would be expected to spawn at the lower end of their range. Indeed, this appeared to happen in *Bathothauma lyromma*. The most dramatic example occurred in *Leachia pacifica*. Young (1975a) demonstrated that this species descends near the time of sexual maturity from near-surface waters to depths of 1,000 to 2,000 m to mate and spawn.

Larvae of most pelagic oceanic cephalopods occur in near-surface waters. Upward migration of larvae would seem to be a formidable task for species that spawn at great depths. The deep-living octopods apparently carry their young partway up presumably to lighten this task. Perhaps squid egg masses are positively buoyant and float to the surface. There are a number of observations of egg masses of pelagic cephalopods floating at or near the ocean surface (see Clarke 1966). However, these have yet to be shown to belong to a deep-spawning species.

Photosensitive Vesicles

These vesicular organs were present in all Hawaiian pelagic cephalopods and they occurred in a great variety of shapes, sizes, and locations. In many squids, the organs were subdivided into as many as four sets of separate organs. In squid, the organs were always found within the confines of the cephalic cartilage and were located either on the optic stalk (central organs) or dorsal, posterior, or ventral to the optic stalk (dorsal, posterior, and ventral organs, respectively). The separate organs often faced different directions (i.e., their broadest surface faced a dorsal, posterior, or ventral direction).

These separate organs were frequently associated with distinctive "windows" in the overlying skin bearing few if any chromatophores. Such windows seem to be unnecessary since most cephalopods can become quite transparent by contraction of their chromatophores. The windows in combination with the more pigmented surrounding skin, however, may restrict light to specific receptors and thereby improve the directionality of the organs. In a few cases (e.g., *Phasmatopsis fisheri* and *Ctenopteryx siculus*), the organ was not subdivided but elongate and curved, allowing different portions of a single organ to face various directions. A directional response of each portion was insured either by heavy pigment (e.g., *P. fisheri*) or silvery iridophores (*C. siculus*) which shielded one surface of the organ. Not all species, however, had vesicular organs that could discriminate between dorsal, posterior, and ventral sources of light. Some species had undivided central organs (e.g., *Sandalops melancholicus*, *Taonius pavo*) without apparent screening devices which therefore are nondirectional. In others, the total area surveyed by a nondirectional organ was restricted by its cryptic position (e.g., *Vampyroteuthis*). Clearly not all cephalopods use these organs in the same way.

General trends between organ size and habitat depth during the day occurred in these animals. Teuthoids and sepioids found in the upper 400 m (neritic species and young *Heteroteuthis hawaiiensis*) generally had small organs. Species found primarily between 400 and 700 m generally had large, complex organs. These included most enoploteuthids, histioteuthids, probably *Discoteuthis laciniosa*, *Liocranchia reinhardti*, and young *Taonius pavo*. Between 700 and 800 m, species with large, complex organs (i.e., *Ctenopteryx siculus*, *Phasmatopsis fisheri*, *Thelidioteuthis allessendrinii*, *Cycloteuthis serventyi*, probably large *Octopoteuthis nielseni*, adult *Taonius pavo*, and *Galiteuthis pacificus*, and *Bathyteuthis abyssicola*) cooccurred with species which had small organs (i.e., chiroteuthids, *Mastigoteuthis*, *Grimalditeuthis bomplandii*, large *Liocranchia valdiviae*, and probably *Neoteuthis* sp.). Many of the small-vesicle species had ranges that extended well below 800 m, where they were joined by other small-organ species (i.e., *Vampyroteuthis infernalis* and probably *Joubiniteuthis portieri*).

The relationship of organ size to habitat depth was especially marked in young *Phasmatopsis fisheri*. The epipelagic larvae of *P. fisheri*, which may grow to 40 and 50 mm ML had small central vesicles. Upon metamorphosis and descent to the adult day habitat (650-775 m), the organs became greatly enlarged (Figure 34). As growth continued, however, a gradual positive allometric growth of the organs occurred without a clear increase in habitat depth.

A number of species did not follow these general trends. Several cranchiids exhibited gradual ontogenetic descent; one of these (*Helicocranchia beebei*) had small organs, while the others (*San-*

dalops melancholicus and *Bathothauma lyromma*) had large organs. *Leachia pacifica*, which had small organs, spent most of its life in epipelagic waters and then descended to depths >1,000 m. *Onychoteuthis compacta* seemed to range widely during the day and had rather large organs (its habitat, however, is poorly known). *Brachioteuthis* had similar organs but probably occurred below 800 m during the day. The ommastrephids had a complex arrangement of organs, yet these animals were primarily epipelagic. In juveniles of many species (e.g., enoploteuthids), the size of the organs (relative to the size of the brain) may be large; yet their absolute size was small when compared with adults occupying the same depths.

Compared with squid, all octopods had small organs. With the probable exception of the tubular eyed *Amphitretus pelagicus*, octopods probably do not occupy depths between 400 and 700 m during the day except as juveniles in transit to greater depths. *Amphitretus pelagicus* is the only pelagic octopod that exhibited clear modification of its organs. In contrast to the small organs, each consisting of a single vesicle, of other octopods, this animal has a larger organ composed of many separate vesicles.

Presumably the general trends with depth were related to depth gradients in both downwelling daylight and bioluminescent light. Downwelling daylight decreases exponentially with depth. Bioluminescent activity should increase from 400 to 600-800 m then decline rapidly if numbers of midwater fishes at various depths (see Amesbury 1975) provide an index to bioluminescent activity during the day. While many vesicles may detect both downwelling skylight and bioluminescent light, we will examine evidence for these two functions separately.

The eyes of some mesopelagic animals can probably detect silhouettes at depths of 750 to 775 m (Young and Roper 1977). Presumably some photosensitive vesicles are at least as sensitive as the eyes, especially when we consider the large size and apparent high pigment density of some (see Young 1972a). The large dorsal organs of squid were positioned so they are exposed to downwelling daylight. Large central organs appeared to be exposed to this light in species lacking dorsal organs.

Some experimental evidence indicates that midwater cephalopods detect downwelling light with these vesicular organs. A number of cephalopods have been seen to conceal themselves with bioluminescent light (Young and Roper 1977). This counterillumination requires that the intensity of downwelling light is precisely determined by the animal, and the photosensitive vesicles seem the likely photoreceptor (Young 1973, 1977). Recently R. E. Young, C. F. E. Roper, and J. Walters (in manuscr.) covered the dorsal organs of *Abraliopsis* sp. B while it was counterilluminating and recorded a 90% drop in its luminescence. They concluded that the dorsal organs detect downwelling light. Since animals can detect downwelling light with these organs for counterillumination, they may use this photic information for other purposes as well.

Vertical migration in many midwater animals is closely associated with changing light levels (Boden and Kampa 1967). Since cephalopods migrate during twilight periods, light cues received by the vesicular organs may serve to trigger or regulate their migrations. This view is supported by three sources of evidence. First, nerves from the vesicles pass into the peduncle complex of the brain. Messenger (1967b) suggested, on the basis of experimental evidence in *Octopus*, that this complex is part of a visuomotor system: visual information from the eyes enables this complex to exercise control over locomotion. Secondly, experimental evidence on the function of the photosensitive vesicles in neritic *Octopus* strongly suggests that these organs regulate diurnal activity patterns (R. Houck pers. commun.). Finally, most migrating cephalopods have large vesicular organs positioned to detect downwelling light. The only exceptions are species of *Mastigoteuthis* and *Chiroteuthis*, whose migration patterns are not as distinct as in other species.

If dorsal and central organs function primarily in the detection of downwelling light, we may have a clue to the peculiar arrangement of vesicular organs in ommastrephids. The ommastrephids were the only squids that had central organs on the dorsal surface of the optic stalk as well as dorsal organs. In *Nototodarus hawaiiensis*, these two organs differ morphologically (the small central organ has large component vesicles and the large dorsal organ has small vesicles), but the organs are adjacent to one another. The structural differences suggest separate functions for the organs, yet their close proximity indicates that both will be exposed to the same source of light. The same argument holds for these organs in other ommastrephids, although the two organs are

somewhat further separated. The ommastrephids have the unusual habit of usually living in epipelagic waters but occasionally descending to great depths (Roper and Young 1975). Perhaps the central organs function in epipelagic waters while the dorsal organs operate only in deep water. Certainly there are considerable problems associated with a single organ functioning over such a wide range of light intensities.

Certain photosensitive vesicles appear to detect bioluminescent light rather than downwelling skylight. The small vesicular organs in the deep-living *Vampyroteuthis infernalis* are shielded from downwelling skylight (Young 1972a). Vesicular organs are present in the blind bathypelagic octopod *Cirrothauma murayi* (J. Z. Young in Packard 1972) which lives in depths where detectable surface light is absent. Certain photosensitive vesicles of many other species were shielded from downwelling light. Such organs presumably detect bioluminescent light. Young (1973, 1977) demonstrated that certain vesicular organs in some species were directly exposed to the animal's photophores, presumably for counterillumination purposes.

The detection of bioluminescence is not limited, however, to the animal's own photophores. With only a few exceptions all species examined had some means of "viewing" various parts of the mantle cavity with their vesicular organs. In many cases, the organs seemed precisely placed for this purpose (see Figure 6). In most species with large opaque livers (e.g., ommastrephids, enoploteuthids, histioteuthids, bathyteuthids, cycloteuthids, octopoteuthids, and mastigoteuthids), some organs extended laterally or ventrally past the liver, enabling a "view" of the mantle cavity. In other species with the liver far back in the mantle cavity (e.g., cranchiids, *Brachioteuthis*, *Ctenopteryx*), only central organs were present. In *Vampyroteuthis infernalis*, the organs lay within the mantle cavity and could only be exposed by light originating within this cavity, the funnel, or at the mantle opening. This animal, like most other cephalopods, had no photophores in these locations. The photosensitive vesicles in octopods were also located within the mantle cavity. The view of the mantle cavity is obscured only in *Onychoteuthis*, *Chiroteuthis*, *Joubiniteuthis*, and Chiroteuthidae gen. sp., although most of these species could still detect light from within the funnel and at the entrance to the mantle cavity.

Young (1972a) suggested that the photosensitive vesicles in *Vampyroteuthis* detect small glowing organisms that are carried into the mantle cavity with the respiratory current. In the deep sea, a glowing organism within the mantle cavity could reveal the squid's location and have disasterous consequences. J. Z. Young (1977) extended this idea to octopods. Nevertheless, this suggestion seems unlikely to have broad application in explaining the consistent relationships between vesicle location and mantle cavity "visibility"; however, no alternative function has been found.

Some squid may detect bioluminescent light originating outside the animal. The large vesicular organs in the deep-living *Bathyteuthis abyssicola* are not exposed to its own photophores and probably detect bioluminescence from animals located outside its restricted visual field (Young 1972a). In *Ctenopteryx siculus*, the elongate vesicular organs joined in the midventral line over the funnel and were there shielded dorsally and laterally by a thick layer of iridophores. The ventral part of this organ would detect light originating within the funnel. Yet, the high organization and sophisticated structure of the vesicles seem overly matched for such a task. This organ probably "looks" ventrally through the funnel to the area below the squid. Similar arguments could be made for certain lobes in other squids.

The photosensitive vesicles in many cephalopods apparently form an elaborate system for monitoring bioluminescent light from their own photophores, from within the mantle cavity, and from the immediate vicinity of the animal that lies outside the visual field

The great variety of photosensitive vesicles found among the species of pelagic cephalopods off Hawaii presumably reflects a variety of functions for these organs associated with the detection of both downwelling and bioluminescent light. The morphology and placement of these organs have provided some clues to these functions. A full understanding of this complex sensory system, however, must await experimental studies on living animals.

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Note added in proof: The correct name for the species listed here as *Phasmatopsis fisheri* is *Megalocranchia fisheri* (N. Voss. In press. Studies on the cephalopod family Cranchiidae. A revision of the genera, with a key for their determination. Bull. Mar. Sci.)

SYSTEMATIC SAMPLING IN A PLANKTONIC ECOSYSTEM

E. L. VENRICK[1]

ABSTRACT

Two sampling studies, computer simulation and field, investigated the consequences of applying restricted systematic sampling (at predetermined depths) to estimate total chlorophyll in the water column. Comparison was made with stratified random designs with one and two samples per strata. Systematic sampling appeared more accurate than most stratified random designs. However, when repeated over restricted spatial or temporal intervals, systematic designs tended to produce biased estimates. In the central Pacific, an interval of several days, or 100-200 km, appeared necessary for natural population fluctuations to average out the bias inherent in a restricted systematic sampling design.

Underlying sampling theory is the assumption of random collection of samples. This is the only satisfactory method of assuring a representative sample from an unknown population. In pelagic ecology (and undoubtedly in other fields) this assumption is generally neglected and surveys are conducted at fixed geographic positions, at fixed spatial or temporal intervals, and/or at fixed depths, without recourse to randomization. The implicit assumption is that the natural complex variability of pelagic populations provides the necessary element of randomization.

Two types of sampling strategies are frequently called systematic. The present study is concerned with the situation in which the sampling positions are fixed according to some pattern determined by the investigator and are not necessarily at equal intervals; this will be termed restricted systematic sampling (RSS) to distinguish it from the strategy in which only the sampling interval is fixed and the location of the first sample in the first interval is determined at random (randomly located systematic sampling; Yates 1948). Among the alternate sampling strategies which provide the requisite randomization, unrestricted random and stratified random sampling (SR) have received the most attention. In unrestricted random sampling, samples are selected individually from the entire population by some random process, such as by numbering all sampling units and selecting from them by means of a random numbers table. In SR, the population is first divided into subpopulations from each of which one or more samples are selected at random. SR is useful because it ensures that the samples are distributed throughout the entire population.

Three characteristics of sampling designs are of interest (Figure 1): 1) bias, any consistent deviation between the true population parameter and repeated estimates based on the same sampling design; 2) precision, the variability of successive estimates about their mean when a sampling design is repeated on the same population; and 3)

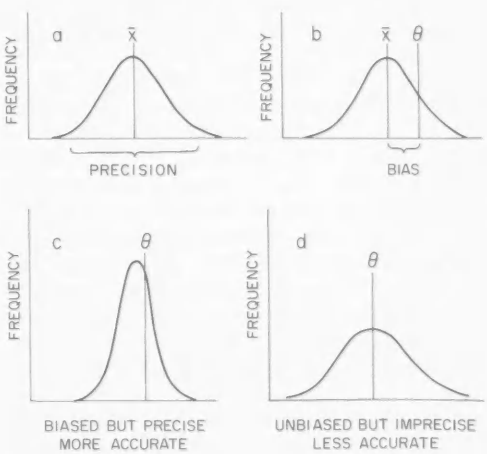

FIGURE 1.—Normal frequency distributions used to illustrate: a) precision, the spread of observations about their mean value ($\bar{x}$); b) bias, the deviation of the mean of repeated observations from the true parameter (θ); c) a distribution which is biased but precise; and d) a distribution which is unbiased but imprecise. Distribution c will be more accurate than distribution d, in spite of the bias, if the average deviation of observations from θ is smaller.

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accuracy, a concept including both freedom from bias and high precision and which, in the absence of bias, is equivalent to precision. The practical determination of precision, in its strictest sense, is restricted to quasi-static populations in which the population remains unchanged between collections of replicate samples (forests or soil types or mussel beds, etc.). In the case of RSS, the concept of precision has no meaning in this type of population because successive application of the same sampling design to the same population will give identical results. Such static populations do not exist in a planktonic system because spatial and temporal variability produce continual change. Thus, in the present study, the concept of a population is expanded to incorporate spatial and temporal fluctuations in which case the precision of RSS has a real value.

Theoretical aspects of systematic random sampling strategies have been considered by many (e.g., Yates 1946, 1953; Deming 1950; Cochran 1963; Sukhatme and Sukhatme 1970). Empirical investigations have been restricted to terrestrial systems, particularly to surveys of vegetation types or timber volumes (e.g., Hasel 1938; Osborne 1942; Finney 1948b, 1950; Numata and Nobuhara 1952; Bourdeau 1953; Milne 1959). The results from these studies indicate that randomly located systematic sampling often gives more accurate estimates than other procedures (Hasel 1938; Osborne 1942; Madow 1946; Yates 1946, 1948; Finney 1948a; Bordeau 1953; Milne 1959; Grieg-Smith 1964) especially when the sampled population has positive correlation between neighboring units (Cochran 1946; Milne 1959; Sukhatme and Sukhatme 1970). Because of the greater precision and greater convenience of systematic sampling, some workers have recommended its use for terrestrial surveys (Hasel 1938; Yates 1946; Milne 1959). On the other hand, it has been shown that irregular distributions or pronounced patterns of variation, especially periodicity or linear trends, may cause systematic designs to give biased estimates or estimates of reduced precision (Madow and Madow 1944; Finney 1950; Bourdeau 1953; Sukhatme and Sukhatme 1970); nor does the precision necessarily improve with increasing sample size (Madow 1946; Bordeau 1953).

Of the random designs, SR generally offers greater precision than unrestricted random sampling (Yates 1953; Milne 1959) and, with a constant number of samples, this precision increases as the number of strata increases (Yates 1953). The most precise design is one with one sample per strata, but this (like a systematic sample) offers no internal estimate of error (Finney 1948a, b).

The success of systematic sampling clearly depends upon the nature of the sampled population. If individuals or properties in a population are distributed at random, all strategies will be equivalent. Pronounced pattern, however, may increase or decrease the effectiveness of systematic designs. Thus, quite aside from the theoretical objections to systematic sampling, uninformed application of any systematic sampling is to be discouraged.

Although Strickland (1968) warned that discrete samples may give a poor representation of the vertical distributions of highly stratified substances, such as chlorophyll, a thorough study of the consequences of systematic sampling in the ocean has not been conducted, even though most populations have marked gradients, especially along the vertical axis. This may be attributed to the logistical difficulties of enumerating an oceanic population in its entirety, in contrast to a timber stand in which every individual may be observed, counted, measured, and mapped.

The present study is restricted to the consequences of applying RSS in the vertical direction. The distribution investigated is that of chlorophyll in an oligotrophic oceanic environment. Total chlorophyll in the water column is a frequently used index of plant crop and it is most often estimated from a series of restricted systematic samples. The major question is whether such sampling produces any bias in the estimate of total chlorophyll, or whether the temporal and spatial heterogeneity of the chlorophyll distribution is sufficient to average out the biases of individual determinations. Of secondary concern is whether there is a significant difference in precision or accuracy between estimates derived from RSS and those derived from SR.

The area of study is the North Pacific Central Gyre in the vicinity of lat. 28°N, long. 155°W. The region is one of relatively low spatial and temporal variability (Venrick et al 1973; Gregg et al. 1973; McGowan and Williams 1973; Eppley et al. 1973; Haury 1976). Thus, it is an environment in which any adverse characteristics of RSS are expected to be magnified. The general features of the distribution of chlorophyll in the North Pacific Central Gyre have been summarized (Venrick et al. 1973). Most of the year, surface concentrations are low (0.02-0.06 mg/m^3), and there is a narrow subsur-

face maximum layer (0.10-0.20 mg/m^3) centered between 90 and 120 m.

The present study was conducted in two parts. In part A, a computer was used to sample nine semiartificial populations derived from continuous vertical profiles of chlorophyll fluorescence. Changes in the fluorescence per extractable chlorophyll unit with depth (Kiefer 1973) and smoothing of small-scale features during the pumping procedure result in a profile which represents only the grosser features of the true distribution. From the vertical profiles, the total population along the vertical axis was calculated, allowing the accuracy of various sampling strategies to be determined directly. Study B was conducted in the field where restricted systematic and stratified random samples were collected simultaneously from the population. In this study, a real population was studied but the total population could only be approximated.

METHODS

Analytical Procedures

Chlorophyll a was determined fluorometrically according to the procedure of Yentsch and Menzel (1963) as modified by Holm-Hansen et al. (1965). Water for discrete, extracted chlorophyll samples was obtained with Nansen bottles. Water for continuous vertical profiles was obtained with the seawater pumping system described by Beers et al. (1967) and was passed through a fluorometer equipped with a flowthrough door.

Study A

The chlorophyll fluorescence profiles were taken during September 1968, on 9 consecutive days during which time the ship followed two drogues which were set at 10 m depth to follow the mixed layer. These were launched at lat. 27°00′N, long. 155°18′W and moved in a northwesterly direction at speeds between 0.5 and 1.5 kn covering 345 km in 9 days. The profiles were not made at the same time of day. The closest two profiles were separated by 13 h, the most distant by 40 h. Additional aspects of these profiles and accessory data have been published (Scripps Institution of Oceanography 1974).

The fluorescence profiles were read at 1-m intervals and translated into units of approximate chlorophyll down to a depth of 180 m. In order to offset the increase in fluorescence per unit of extractable chlorophyll with depth, one conversion equation was used down to and including the chlorophyll maximum and another below the maximum. The conversion factors were determined by analysis of chlorophyll extracted from discrete water samples collected periodically during the cruise. The surface value of each continuous profile was set to 0.03 mg/m^3 and the minimum value below the maximum to 0.01 mg/m^3; these were the mean values of extracted chlorophyll observed at the surface and at 200 m, respectively. The horizontal scale was adjusted to bring the mean maximum value of all profiles to 0.156 mg/m^3, the average maximum of the discrete samples. A typical adjusted profile is presented in Figure 2.

These semi-artificial populations were sampled with four stratified random designs (Table 1). The success of SR depends upon the extent to which the strata can be made internally homogeneous. In an attempt to achieve this, the stratum boundaries of SR-1 and SR-2 were determined as much as possible by the hydrographic, biological, and chemical

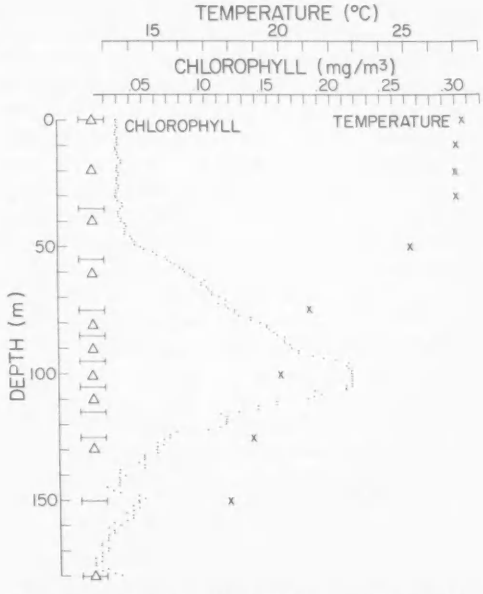

FIGURE 2.—A typical population of chlorophyll values derived from a continuous profile of fluorescence (27 September 1968) and sampled in study A, together with the temperature values from the associated hydrocast. Triangles indicate the location of samples in restricted systematic design 3; bars represent the boundaries of strata used in stratified random design 1.

TABLE 1.—Systematic and stratified random sampling designs used in studies A and B.

Systematic:	RSS-1	RSS-2	RSS-3	RSS-4	Stratified random:	SR-1	SR-2	SR-3	SR-4
	0	0	0	0		0	0	0	0
	20	10	20	45		35	75	15	45
	40	25	40	65		55	95	45	90
Sample	60	35	60	80	Stratum	75	105	75	110
depths	80	50	80	90	boundaries	85	125	90	130
(m)	100	60	90	100	(m)	95	180	100	180
	120	75	100	110		105		110	
	140	100	110	120		115		120	
	160	125	130	137		125		130	
	180	180	180	180		150		150	
						180		180	

characteristics of the environment (Figure 2), and larger strata were assigned to the layers in which environmental gradients were small and several narrow strata were placed in the region of the chlorophyll maximum. The 35-m boundary marked the average depth of the mixed layer; 95 m was the approximate depth of penetration of 1% of the surface radiation, and 125 m represented the beginning of the nutricline. Design SR-1 consisted of 10 strata, each with one sample; in design SR-2, adjacent strata were lumped giving five strata with two samples in each. Designs SR-3 and SR-4 were those used in study B (below) and were thus based on environmental characteristics observed at that time. Each of the nine populations was sampled 20 times with each of the stratified random designs. To facilitate comparison with the systematic samples, for which there was only one cast of each design per profile, it was desirable to examine a series of unreplicated stratified random samples. For this purpose, 10 subsets were selected at random from the replicate casts, each subset containing nine stratified random casts, one from each population. Total chlorophyll was calculated from the mean (arithmetic) concentration per strata times the width of that strata, summed over all strata. This is the classical procedure for summarizing data collected by SR.

Four RSS designs were employed: RSS-1, one sample at the surface and every 20 m thereafter; RSS-2, the design actually employed in September 1968 in which the cast was partially determined by standard hydrographic depths; RSS-3, a design which was based upon complete knowledge of the vertical distributions which were being sampled and which was derived from application of the general rules of sample allocation, i.e., samples were concentrated in the region of maximum variability (the chlorophyll maximum layer); RSS-4, a design based on stratified random design 1 (and therefore more strictly comparable to it) with a sample at the top of the upper stratum (0 m) and bottom of the lowest stratum (180 m) and at the center of all intermediate strata.

Two methods of calculating total chlorophyll from systematic samples were investigated. In the first, the layer between adjacent samples was represented by the arithmetic mean of the two samples (equivalent to integration with linear interpolation). In the second, the layer was represented by the geometric mean of adjacent samples. This latter procedure is sometimes recommended when the population exhibits large, nonlinear changes between adjacent samples. A comparison of the two procedures was made in study A, on the basis of which the method using geometric means was rejected.

Study B

Study B, conducted in June 1977, combined two 10-sample designs, one restricted systematic (RSS-1) and one stratified random (SR-3 or SR-4) into a single 20-bottle cast. The strata boundaries were primarily determined from two preliminary 18-bottle casts which defined the regions of chlorophyll gradients and from a single STD trace which defined hydrographic strata (Figure 3). As in study A, narrower strata were established at the depths of maximum gradients of chlorophyll (the region of the maximum layer). The major differences between designs SR-1 and SR-2 and designs SR-3 and SR-4 were due to a shallower mixed layer and broader, deeper maximum layer observed in June 1977.

Over a period of 21 days, a total of 18 casts were made, 9 employing RSS-1 and SR-3 and 9 employing RSS-1 and SR-4. All casts were located within a rectangle bounded by lat. 28°21.6′N and 28°45.9′N, and by long. 155°14.0′W and 155°33.5′W. Fourteen casts were taken in conjunction with another program between the hours of 2200 and 0300 (with one exception, delayed by winch failure until 0550). Twelve casts were

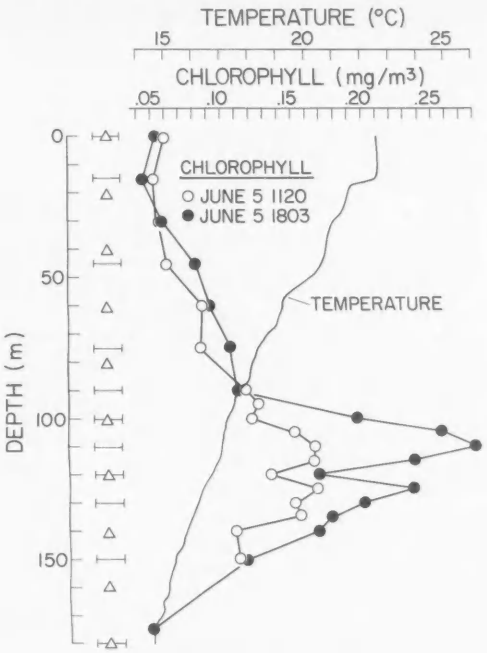

FIGURE 3.—Chlorophyll values observed in two 18-bottle casts preliminary to study B, together with the temperature trace from the associated STD lowering. Triangles indicate location of samples in restricted systematic design 1; bars represent the boundaries of strata used in stratified random design 3.

paired, taken within a few hours and within 3 n.mi. of each other. These have been considered replicate casts.

When the combined systematic-stratified random design called for bottles to be spaced more closely than 3 m, it was necessary to use a messenger heavier than the standard Nansen messenger (such as a Niskin bottle messenger) in order that it develop enough momentum to trip the second bottle. When both sampling designs called for the same depth, the extra bottle was arbitrarily positioned, usually filling in the largest gap in the region of the chlorophyll maximum layer. This "free" sample was used only in the calculations of total chlorophyll in the water column.

Statistical Procedures

Bias is evaluated by the consistency with which n observations ($x_i, i = 1, n$) from a given sampling design fall above or below the true population value and may be measured as a percent of the true value (θ):

$$\left[\frac{\sum (x_i - \theta)}{n} \times 100\%\right] / \theta.$$

Precision is measured by the variance of a series of n observations about their mean ($\bar{x}$):

$$\frac{\sum (x_i - \bar{x})^2}{n-1}.$$

In an analogous way, accuracy is measured by the mean square deviation of a series of observations from the true population total:

$$\frac{\sum (x_i - \theta)^2}{n-1}.$$

Both accuracy and precision are inversely related to their statistical measures, increasing as the numerical value of the measure decreases. Since most scientists are used to thinking in terms of variances and sums of squares, it did not seem desirable to invert these measures to achieve direct correspondence.

In the analysis of the results, limited use was made of the parametric analysis of variance. Most statistical tests were nonparametric tests which make few assumptions about the characteristics of the data (e.g., Dixon and Massey 1957; Tate and Clelland 1957; Conover 1971; Hollander and Wolfe 1973). Unless stated otherwise, the probabilities associated with conclusions in the text are derived from the binomial distribution with $p = ½$.

In several analyses in these studies, the problem of multiple testing arose, as when all four systematic designs were tested for bias. Unfortunately, the tabulation on most nonparametric procedures is not sufficiently complete to allow correction for multiple testing to be made without making the tests extremely conservative. Since this was deemed undesirable, the probabilities given for the statistical tests are uncorrected. It is unlikely that this makes any real difference in the outcome of these studies which gain most of their force from the similarity of results in the two approaches.

RESULTS

Study A

Integration of values

The results of study A are summarized in Table 2. The total chlorophyll values derived from the four systematic sample designs were calculated by integration with linear interpolation (i.e., using the arithmetic mean of adjacent samples to represent the average chlorophyll in the stratum between them). Use of the geometric mean in this calculation resulted in the true total being underestimated 27 out of 36 times ($P = 0.01$). Nor was there any increase in accuracy (the resultant accuracies, based on use of the geometric mean, were 0.538, 0.987, 0.488, and 0.752 for RSS-1 through RSS-4). The use of the geometric mean in the calculation of total chlorophyll does not appear to be justified.

Bias

The biases observed in the eight sampling strategies are summarized in Table 3. Of the four restricted systematic designs, only RSS-2 gave no signs of bias. Design RSS-3, the "best informed" design, overestimated the true population total in eight of the nine trials ($P<0.05$). RSS-1 overestimated the population only five out of nine times, but the overestimates were clustered toward the end of the series and the underestimates toward the beginning. This temporal trend lies just outside the usual level of significance (run test; $P<0.10$) but it indicates that the time period necessary for the population to provide "random" variability of sufficient magnitude to eliminate bias may be of the order of several days or 100-200 km. The magnitudes of the biases were −4.0% for the period 19-21 September and +3.7% for the period 24-27 September. Similarly, the bias introduced by using RSS-3 to estimate the true population total for 19-25 September was −3.6%.

The peculiar periodicity of bias seen in RSS-4 also indicates a nonrandom interaction between the sampling design and the sampled population

TABLE 3.—Bias of systematic and stratified random sampling designs, Study A.

Date (1968)	Systematic designs				Stratified random designs			
	RSS-1	RSS-2	RSS-3	RSS-4	SR-1	SR-2	SR-3	SR-4
19 Sept.	−	−	+	−	+	− −	−	+
20 Sept.	−	−	+	+	−	− +	[1]0	−
21 Sept	−	−	+	−	+	− +	[1]0	+
22 Sept.	+	+	+	+	−	− +	[1]0	+
23 Sept.	−	−	+	−	−	− −	−	−
24 Sept.	+	−	+	+	+	− −	+	+
25 Sept.	+	+	+	[1]0	−	− −	−	+
26 Sept.	+	−	−	−	+	− +	−	+
27 Sept.	+	+	+	+	+	− +	+	−

[1]Estimate = true value.

TABLE 2.—Results of study A, a computerized simulation sampling study. The estimated parameter (θ) is total chlorophyll above 180 m; units are milligrams per square meter; time is local time.

Date (1968)	Time	True value (θ)	Systematic designs One cast each				Stratified random designs Means and variances (in parentheses) of 20 replicates			
			RSS-1	RSS-2	RSS-3	RSS-4	SR-1	SR-2	SR-3	SR-4
19 Sept.	1719	8.50	8.00	8.00	8.62	8.39	8.52	8.38	8.39	8.59
							(0.345)	(2.460)	(0.642)	(0.050)
20 Sept.	2312	10.31	9.91	9.98	11.12	10.71	10.29	10.18	10.31	10.24
							(0.244)	(0.987)	(0.182)	(0.513)
21 Sept.	2335	7.35	7.21	6.69	7.57	7.33	7.36	7.16	7.35	7.36
							(0.059)	(0.950)	(0.215)	(0.466)
22 Sept.	2351	6.89	7.23	7.72	7.45	7.18	6.85	6.88	6.89	6.92
							(0.072)	(0.151)	(0.080)	(0.129)
23 Sept.	2025	8.83	7.97	7.51	9.03	8.47	8.62	8.68	8.82	8.78
							(0.801)	(1.780)	(0.341)	(1.227)
24 Sept.	0900	9.68	9.70	9.20	9.94	10.56	9.81	9.57	9.85	9.79
							(0.178)	(1.490)	(0.406)	(1.841)
25 Sept.	0800	11.00	11.84	12.08	11.08	11.00	10.86	10.90	10.92	11.16
							(0.263)	(1.436)	(0.443)	(0.687)
26 Sept.	0830	13.85	14.23	13.14	13.36	13.06	13.92	13.23	13.65	13.90
							(1.123)	(5.323)	(2.289)	(3.954)
27 Sept.	2400	13.90	14.47	14.56	14.94	14.78	14.17	13.60	14.06	13.83
							(0.490)	(3.676)	(1.409)	(3.348)
Accuracy $\frac{\sum(x_i - \theta)^2}{n-1}$			0.308	0.695	0.308	0.320	[1]0.574	[1]1.464	[1]0.779	[1]1.662
Precision $\frac{\sum(x_i - \bar{x})^2}{n-1}$		6.441	8.113	7.729	6.537	6.725	[1]8.004	[1]6.312	[1]7.036	[1]8.540

[1]Mean values from 10 sets of unreplicated casts.

(run test, $P = 0.10$). With the sampling interval employed here, the biases of individual estimates average out over the entire study. Had the interval been twice as large, a consistent overestimate or underestimate would have resulted, with respective magnitudes of +5.8% and −1.9%, until 25 September when the phase relationship appears to have shifted.

Tables 2 and 3 also present the results of the four stratified random designs, based upon the means of 20 replicates. The consistent underestimates resulting from SR-2 were sufficiently unexpected that a second series of 20 SR-2 samples were drawn from each population. This series showed no evidence of bias and, thus, it appears that the initial results were the product of random chance.

Precision

Precision, in its strictest sense, could only be examined in the case of the stratified random designs, for which replicates were available. The designs employing 10 strata, each with one sample, SR-1 and SR-3, offered greater precision than designs with fewer strata. However, there was a highly significant concordance (Kendell coefficient, $P<0.01$) between the precisions of all designs with respect to the profiles giving the most precise result. Examination of the individual profiles indicated that the precision of the results was inversely related to the strength of the chlorophyll maximum and to the amount of small-scale variability along the vertical axis, or, in other words, to the structural complexity of the population. Later, the accuracy of the systematic designs (discussed below) was found to show the same relationship.

For all stratified random designs, the variance between replicates was trivial compared with the variance between the nine populations. Analyses of variance gave $f_{8,19}$ ratios ranging from 54 to 344 (all $P<<0.01$). When all nine profiles were considered to be replicates of the same population, the variance between the nine estimates from each systematic cast could be compared with the variance between single stratified random casts, one from each population (Figure 4A). On this scale, there were no differences in precision between any of the sampling designs. The large variation between populations masked any difference in performance. Thus, when the concept of the sampled population is expanded to include spatial and temporal variations, RSS appears to offer neither advantages nor disadvantages with respect to precision of estimates.

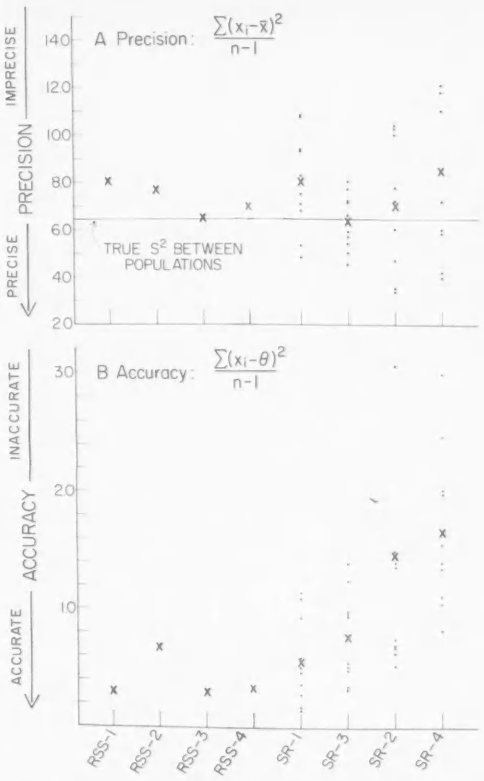

FIGURE 4.—The results of the computer simulation sampling study, study A, showing the relative precisions and accuracies of the four restricted systematic sampling designs (RSS) and four stratified random designs (SR).

Accuracy

The accuracy of the various designs was also compared using sets of unreplicated stratified random casts (Figure 4B). The greater accuracies of stratified random designs SR-1 and SR-3 relative to SR-2 and SR-4 undoubtedly reflected their greater precision; and perhaps the greater accuracy of SR-1 relative to SR-3 was due to selection of more appropriate strata. The systematic designs were generally more accurate than the stratified random designs. Only stratified random design SR-1 achieved the accuracy of the systematic designs.

Most of the chlorophyll work in the central Pacific has been based upon 12 or more sampled depths. Thus, it was encouraging to find that as few as 10 depths, regardless of the sampling strategy, gave a generally satisfactory picture of the amount of chlorophyll in the water column. Of nearly 400 estimates from individual casts, 76% fell within ±10% of the true value. This percent increased to 85% for stratified designs SR-1 and SR-3 and to 94% for the 36 systematic casts. However, to the extent that these fluorescence profiles underestimate the structural complexity of the true chlorophyll distribution, these results probably overestimate the accuracies of the designs.

Study B

The results of the field study were remarkably similar to those of the computer study (Table 4). Bias and accuracy were investigated by assuming that the entire population was exactly represented by the 20 samples in one cast (systematic samples plus stratified random samples plus "free" samples). The results of study A indicate that the discrepancy is not likely to be severe.

Bias

When the 18 casts are considered in chronological sequence, it is evident that RSS tended to deviate from the true value in the same direction on adjacent casts. The direction of bias was the same within five of the six pairs of replicate casts ($0.05<P<0.10$) and a run test over the entire sequence was significant ($P = 0.05$). The absolute magnitude of the bias which would result were the five replicate pairs considered estimates of five population totals ranged from 0.3% to 3.7% with a mean of 2.0%. Within the restricted spatial area of this survey, between 2 and 8 days appear necessary for the natural fluctuations of the population to be sufficient to average out bias inherent in RSS.

Precision

Precision was investigated by means of the six pairs of replicate casts. Stratified random design SR-3 with one sample per strata was more precise than the design with two samples per strata ($f_{3,3} = 6.5$, $P<0.10$). The precision of the systematic design was intermediate and was not significantly different from either.

TABLE 4.—Results of study B, a field sampling study. The estimated parameter is total chlorophyll above 180 m and the true value (θ) is estimated from the 20 combined samples of the two designs; units are milligrams per cubic meter.

Date (1977)	Local time	θ	x_i bias RSS-1	x_i bias SR-3	x_i bias SR-4
5 June]	2345	18.87	18.73−	18.25−	
5 June]	0220	17.68	17.10−	18.69+	
8 June	0033	15.54	14.06−	18.21+	
9 June	0236	18.11	17.23−	17.55−	
9 June]	2241	16.70	16.22−	17.19+	
10 June]	0550	15.47	14.75−	16.68+	
13 June]	2208	13.26	13.29+	12.31−	
14 June]	0035	13.42	13.47+	13.33−	
15 June	2203	14.53	15.91+	11.19−	
19 June]	2149	11.50	10.91−		9.03−
20 June]	0100	10.29	10.78+		10.78+
21 June	2246	14.25	14.73+		11.42−
22 June	1107	10.67	11.00+		10.17−
23 June]	2333	13.60	13.41−		12.97−
24 June]	0133	12.52	12.16−		12.09−
24 June]	1505	16.83	17.11+		18.11+
24 June]	1632	16.98	17.69+		15.72−
26 June	0822	13.32	13.58+		13.10−
Accuracy:	$\frac{\sum(x_i - \theta)^2}{n-1}$		0.45	2.83	2.31
Precision	(6/5-6/15)	0.492	0.808	0.249	
MS w/in pairs] :	(6/19-6/25)	0.442	0.319		1.591

] indicates pair of replicate casts.

Accuracy

The accuracies of the two stratified random designs, as measured against the total chlorophyll estimated from all 20 samples, were similar, but the systematic design RSS-1 was significantly more accurate than either (signed rank test, $P<0.05$). Possibly the greater accuracy of the systematic designs, seen in both studies, might be partially attributable to the different arithmetic formulae with which total chlorophyll was calculated since these give somewhat different weights to the individual samples. To test this, the estimates from both the restricted systematic and the stratified random designs were calculated by linear integration. This did not alter the relative accuracies of RSS-1 and SR-3 in study B or of RSS-1 and SR-1 in study A, nor did it eliminate the bias apparent in RSS-1. Thus, it appears to be the sample location rather than the formula by which total chlorophyll is calculated that is responsible for the greater accuracies of the systematic designs.

DISCUSSION

These studies indicate that there is a potential for biased estimates to be derived from systematic samples collected from a planktonic ecosystem.

While it is recognized that the results suffer from small sample sizes, they gain considerable force from the fact that two different approaches give quite similar conclusions.

It appears that RSS, when applied to the vertical distribution of chlorophyll, may actually give estimates of total chlorophyll which are, on the average, closer to the true value than are estimates based on SR. This is consistent with results from terrestrial systems. Stratified random designs frequently result in pairs of samples falling closely adjacent to one another. In populations which are varying continuously, the information contained in such an adjacent pair is largely repetitious. Such redundancy is avoided in RSS because the spacing between adjacent samples is controlled. The relative performance of SR is expected to improve in populations with more discontinuous distributions such that the strata may be defined to be internally homogeneous, giving maximum precision. On the other hand, and perhaps more important, there appears to be a potential for bias in systematic designs, especially when the sampling occurs within restricted spatial or temporal intervals. In the central Pacific, which is relatively homogeneous in time and space, the bias was detectable, but the magnitude was small. Unfortunately, the results cannot be generalized to other environments. The bias may be expected to diminish as increasing environmental complexity increases the small-scale variability of the sampled population. Whether or not bias is therefore negligible in more complicated neritic environments remains to be investigated.

On the other hand, in planktonic environments the natural fluctuations produce variability between replicate casts which is generally large relative to the experimental error associated with a single cast. The increased accuracy of systematic designs is not likely to result in a detectable increase in the precision of the estimate of the mean of several samples. Depending upon the goals of a study, it may also be true that the magnitude of the bias introduced by systematic sampling is insignificant. For instance, it appears that RSS as routinely used on large-scale oceanic surveys probably introduces no serious error. However, increasing attention is being focused on small-scale, local phenomena, and the routine use of RSS for these studies deserves examination. Possible effects of the interaction between bias and sampling scale found in this study include overestimation of fluctuations in total population (if a positive bias occurs with higher populations and a negative bias with lower populations), underestimation of fluctuations (if a positive bias occurs with lower populations and a negative bias with higher populations), or production of artificial fluctuations when in fact the population is stable. Whether or not such artificial effects of RSS might be important enough to overshadow the gain afforded in terms of ease of sample location and data analysis depends upon the particular study under consideration.

Study A demonstrated the dependence of the success of a sampling design upon the interaction of that design with the structure of the population being sampled; thus, it would seem that intelligent application of knowledge about the sampled population should improve the design. It was, therefore, disconcerting to find that RSS every 20 m, RSS-1, consistently performed as successfully as did RSS-3 which was designed by a presumably experienced worker (the author) with total knowledge about the population to be sampled. We must conclude either that the location of samples in RSS-3 was not as intelligent as it might have been, or that the natural variability of the population makes intelligent placement of systematic samples impossible. (The latter interpretation has a certain appeal.) In contrast, the dependence of SR on the selection of strata is apparent in both studies. Many narrow strata give more precise and accurate estimates than do fewer, larger ones, undoubtedly because, in the presence of strong vertical gradients, they better satisfy the criterion of internal homogeneity. The most precise and accurate results are obtained when the number of strata is equal to the number of samples. The disadvantage of this strategy is the absence of direct estimates of variability within strata from which to calculate confidence intervals around the final estimate. This is not usually of concern in planktonic work because small-scale patchiness is of such magnitude that more useful estimates of precision are obtained directly from replicate casts, and thus apply to some spatial and temporal interval, rather than to a single cast.

The logistics of SR in the open ocean presented few major difficulties. The task of allotting samples randomly to strata was time consuming. After the first few casts, the job of sample design was relegated to the computer. Preparation of the cast card demanded more than routine caution (although minor errors were readily assimilated into the randomization procedure). The use of random

sampling also precluded routine sharing of water samples with others whose programs were designed around standard depths, and, with the present high cost of ship time, the pressure for sharing samples is often considerable. Indeed, this study was possible primarily because there was an unusual amount of excess wire time available.

On the other hand, there were advantages to SR quite apart from the general merriment caused by the unorthodox bottle spacing. The results from the occasional closely spaced samples gave continual insight into the vagueries of small-scale vertical stratification. For instance, within the top 30 m, samples separated by 1- and 2-m intervals differed by <3% of their mean. In the region of the chlorophyll maximum, between 75 and 125 m, the same intervals produced deviations of 30% and 40%, indicating sharp layers and frequent inversions.

It is not within the scope of this paper to make generalizations concerning the use of systematic sampling versus SR. The potential advantages and disadvantages of each have been demonstrated in one environment. It is the responsibility of all researchers to evaluate the use of RSS in reference to their specific programs. If a potential problem is recognized, it is hoped that it will stimulate a preliminary sampling study to examine directly the consequences of RSS in the biological system of interest. This worker's experience with SR was satisfactory, and the potential for biased data is sufficiently undesirable that effort will be made to incorporate randomization into future sampling designs. It is hoped that the untidy profiles which will result will be accepted with understanding by the scientific community.

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DISTRIBUTION AND ABUNDANCE OF SMALL FLATFISHES AND OTHER DEMERSAL FISHES IN A REGION OF DIVERSE SEDIMENTS AND BATHYMETRY OFF OREGON

WILLIAM G. PEARCY[1]

ABSTRACT

Demersal fishes were sampled at seven stations located inshore of Heceta Bank, on Oregon's continental shelf, over a 2-yr period with a 3-m beam trawl designed to catch small flatfishes. Two general assemblages of fishes were recognized: a shallow water (74-102 m), sandy-bottom association where Pacific sanddab, *Citharichthys sordidus*, was numerically the dominant species, and a deeper (148-195 m) assemblage, generally on mud, where the slender sole, *Lyopsetta exilis*, predominated. Rex sole, *Glyptocephalus zachirus*, was usually the second most common species at all stations. Dover sole, *Microstomus pacificus*, ranked fourth to sixth by numbers and composed the largest biomass (wet preserved weight) at three stations. Species diversity was lowest at the shallowest station where sediments were well-sorted, fine sands that contained only 0.1% organic carbon.

The biomass of all fishes captured ranged from 0.9 to 2.4 g m^{-2}. These values are low compared with estimates made by others off Oregon and Washington using commercial-sized otter trawls, presumably because of avoidance of the small beam trawl by large fishes.

An analysis of variance of the catches of all fishes combined, of Dover, rex, and slender soles, and of Pacific sanddab revealed few significant effects of sediment, depth or season. Sediment type had a significant effect on the catches of slender sole—largest catches were on a clayey-silt bottom. Catches of sanddab were inversely related to depth of water. Depth-season interactions were significant for all species combined and for rex and Dover soles, numbers were higher at the deepwater stations during winter than summer, indicating seasonal bathymetric movements. Annual variations were marked—total catches and catches of most species were larger for unknown reasons during 1968 and 1969 than 1970.

Based on length-frequency data, age-group 0 (<50 mm standard length) rex sole were found in high proportions at the deepest stations on the outer edge of the continental shelf. Small sanddab (<70 mm) composed a larger proportion of the catch by numbers on sandy silt than on sand where larger fish predominated.

Both sediment type and depth of water have been correlated with the abundance and species composition of benthic animals. According to Thorson (1957), the physical and chemical composition of sediments may be the main factor in determining the general pattern of distributions of infaunal and epifaunal invertebrates on the level sea floor. Direct influence of bottom type on demersal fishes may be less than on infauna and epifauna, but sediments may affect fishes indirectly by influencing the composition and abundance of available benthic food. Depth of water has frequently been related to faunal changes of both benthic invertebrates and vertebrates across the continental shelf and slope (Sanders and Hessler 1969; Alton 1972; Haedrich et al. 1975). In some studies, these faunal changes were related to concomittant changes in both sediment type and depth (Day and Pearcy 1968).

The influence of depth and sediments on the distribution of the benthos, however, is difficult to separate because these factors are usually closely correlated. Sediment texture generally decreases with increasing depth of water. Small particles are transported from regions of high energy waves and currents into deep, low energy sedimentary environments, while coarse sediments, such as sands, generally are deposited close to their continental source in shallow water.

This study is an attempt to analyze the relationships between sediment and depth on the species composition of benthic fishes and the abundance of small flatfishes in a localized region, mainly inshore of Heceta Bank along the continental shelf of Oregon. The bathymetry and sediments are variable in this region (Figure 1). This is an important factor in this study because the resulting sediment

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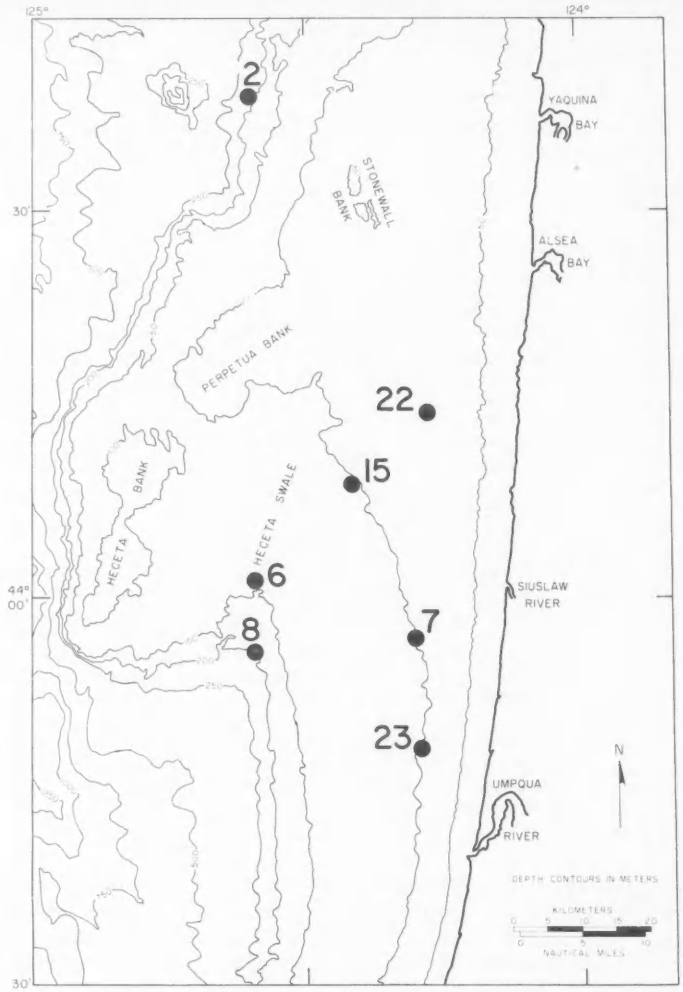

FIGURE 1.—Locations of the seven stations (numbered) off the central Oregon continental shelf that were selected for this study.

types are diverse and do not necessarily grade regularly from coarse sand on the inner shelf to finer sediments with increased depth (Kulm et al. 1975). Because of this heterogenous distribution of sediments, a natural experiment can be designed to differentiate between possible effects of depth and sediment type. Seven stations were selected in an attempt to provide different sediment types at the same depth and the same sediment types at different depths. The region inshore of Heceta Bank produces large commercial catches of flatfishes, such as Dover sole, rex sole, English sole, and Pacific sanddab (Demory et al.[2]).

METHODS

The sediment types for the stations were characterized by the percent sand, silt, and clay, percent of organic carbon and median particle size by Bertrand (1971) and Gunther (1972) (Table 1). A Phleger multiple corer was used to sample sediments. Initially sediments were sampled at the apices of a triangle (sides = 1 n.mi.) and at each

[2]Demory, R. L., M. J. Hosie, N. Ten Eyck, and B. O. Forsberg. 1976. Marine resource surveys on the continental shelf off Oregon, 1971-74. Oreg. Dep. Fish Wildl. Rep., 49 p.

TABLE 1.—Average sediment texture, percent organic carbon,[1] and median particle size[2] at the seven stations off Oregon (from Bertrand 1971). Stations are arranged according to depth.

Item	Station 22 74 m	7 100 m	23 102 m	15 102 m	6 148 m	2 190 m	8 195 m
Clay (%)	0.9	11.7	23.6	7.3	30.3	14.7	35.3
Silt (%)	0.4	22.1	48.1	8.6	66.6	16.8	62.1
Sand (%)	98.7	63.7	28.3	84.1	3.1	68.5	2.6
Organic C (%)	0.1	0.6	1.3	0.4	1.7	1.0	1.6
Median particle size (Md ϕ)	1.88	4.20	6.01	2.99	6.85	4.62	7.22

[1]The percent organic carbon was estimated by the difference in weight between total carbon and calcium carbonate carbon. Total carbon was determined by dry combustion in a Leco induction furnace and measurement of the evolved CO_2 in a Leco gas analyzer. Calcium carbonate was measured by acidifying ground, dried sediment with 0.1 N HCl and measuring the CO_2 evolved (Bertrand 1971). (Reference to trade names does not imply endorsement by the National Fisheries Service, NOAA.)

[2]Mdϕ = ϕ_{50}, where $\phi = -\log_2 D$ and D = diameter in millimeters. See Inman (1952).

station at the center of the triangle. The upper 2 cm of the cores were analyzed. Sediment particle size was measured by standard procedures (Krumbein and Pettijohn 1938). The coarse sand fractions were analyzed by the settling tube method (Emery 1938). Particle size of sediments in the vicinity of each station was similar (Bertrand 1971). Sediments were also sampled at each station during each cruise. According to Gunther (1972), seasonal variations of sediment grain size parameters within stations were not significant, but significantly different sediment types were found among stations at about the same depths, and fairly similar sediments occurred at different depths.

Three station-pairs were identified that had rather similar sediment characteristics but were located at different depths (Table 1): 1) Stations 6 and 8 (148- and 195-m depth, respectively) had highest percentages of clay and silt, lowest percentages of sand, and the highest organic carbon of all stations; 2) Stations 22 and 15 (74 and 102 m) had sandy sediments with low percentages of clay, silt, and organic carbon; Station 22, however, was almost entirely (99%) well-sorted beach sand; 3) Stations 7 and 2 (100 and 190 m) had 60-70% sand and intermediate percentages of clay and silt (12-22%) and organic carbon (0.6 and 1.0%). Station 2 had a thin overlying layer of silt that was absent at Station 7 (Roush 1970); 4) Station 23 located at 102-m depth, about the same as Stations 7 and 15, was intermediate in sediment texture and organic carbon between stations 7 and 2 and 6 and 8. Thus, stations were recognized with three different types of sediment at about 100 m and two different types at 190-195 m. These sediment types agree with three types recognized by Kulm et al. (1975) for the continental shelf off Oregon: 1) well-sorted detrital sands (former beach sands) with a high quartz content mainly on the inner shelf; 2) patchy mud facies largely at midshelf depths and concentrated near large rivers; and 3) mixed sand and mud between the sandy facies and the outer edge of the shelf. Glauconite, the principal authigenic constituent of shelf sands, occurs around the rocky outcrops such as Heceta Bank and along the outer edge of the continental shelf.

Fishes were collected in beam trawls 3 m or 2.7 m wide and 76 cm high at the same seven stations on the central Oregon continental shelf (Figure 1). This net has a small mesh size (13-mm stretch measure) and mouth opening and therefore caught mainly small species and juveniles of most commerical species. A total of 115 tows were made on nine cruises between August 1968 and August 1970. Trawls were made during daylight hours. Each station was sampled during the four seasons of each year. The trawl was streamed at a ship speed of 3.7 km/h (2 kn), and descended at 30 m wire/min until a scope of 1:4 was achieved, towed for about 15 min (mean, 16 min, SD 5.3), and then retrieved at 30 m wire/min. Two beam trawl tows were made at each station during each cruise with standardized trawling procedures by the same personnel.

An odometer wheel was mounted outside of each skid to provide estimates of the distance trawled over the bottom. Area sampled was calculated from the circumference of the odometer wheels, the number of revolutions recorded on odometer counters, and the distance between the skids (see Carey and Heyamoto 1972).

The two odometer readings for a tow were usually similar. Where they differed, I used the highest reading and assumed that slippage of the wheel in sediments or jamming by sea pens, etc. caused the low reading. Rigid stops were mounted on the skid frame to prevent turning of the wheels until they contacted the bottom.

The effectiveness of odometer wheels to estimate distance traversed by the beam trawl on the bottom has been assessed by Carney and Carey.[3] They recognized slippage of the wheels in the sediment and failure of the footrope to effectively tend the bottom at all times as possible errors in measuring actual areas sampled. For these

[3]Carney, R. S., and A. G. Carey, Jr. A report on the effectiveness of metering wheels for measurement of the area sampled by beam trawls. Unpubl. manuscr., 17 p.

reasons, catch per tow was used as a supplementary estimate of abundance in addition to catch per square meter derived from odometer readings.

All fishes were preserved with 10% buffered Formalin[4] at sea, and identified, measured (standard length, SL) and weighed (wet preserved weight) ashore.

RESULTS AND DISCUSSION

Fish Assemblages

The rank order of abundance of the 10 most common species are shown in Table 2. Pacific sanddab, *Citharichthys sordidus*, was the numerical dominant at the four shallowest (74-102 m) stations where it composed 25-86% of the total number of fishes captured. At the three deepest (148-195 m) stations, slender sole, *Lyopsetta exilis*, ranked first in abundance where it composed 38-42% of the number of fishes collected. Rex sole, *Glyptocephalus zachirus*, ranked second in abundance at all stations (except at Station 6 where it was third). The high rank of rex sole at all stations corroborates Hosie's [5] observation that rex sole is probably the most widely distributed sole on the continental shelf and upper slope off Oregon, occupying a large bathymetric range with diverse sediments. Dover sole, *Microstomus pacificus*, ranked fourth at the four inshore stations and fifth or sixth at the deeper stations.

Demory's (1971) study off northern Oregon and southern Washington showed that these flatfishes were most abundant at the following depths:

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[5]Hosie, M. J. 1976. The rex sole. Inf. Rep. 76-2, Oreg. Dep. Fish Wildl., 5 p.

TABLE 2.—Ranks of the 10 most numerically abundant fishes at each of the seven stations, and the presence (+) of these species at other stations if they did not rank among the top 10. Absence of either a number or (+) indicates that a species was not captured at that station.

	Station						
Item	22 74 m	7 100 m	23 102 m	15 102 m	6 148 m	2 190 m	8 195 m
Citharichthys sordidus	1	1	1	1	6	+	4
Glyptocephalus zachirus	2	2	2	2	3	2	2
Microstomus pacificus	4	4	4	4	5	6	6
Lyopsetta exilis	8	5	6	6	1	1	1
Lycodopsis pacificus	+	3	3	10	2	8	3
Xeneretmus latifrons	+	+		+	4	3	7
Cymatogaster aggregata	5	6	7	3	+		
Parophrys vetulus	3	10	8	5			+
Sebastes juveniles					7	5	5
Eopsetta jordani	6	9	+	+	+		+
Sebastes crameri		7	5	+	9	10	10
Asterotheca pentacanthus			+		+	4	+
Poroclinus rothrocki		8	9	+	+		8
Thaleichthys pacificus	9	+	+	+	+	7	+
Allosmerus elongatus				7			
Icelinus borealis	7						
Merluccius productus		+	+	+	8	+	+
Sebastes elongatus					+	+	9
Radulinus asprellus	+	+	+	8	+		
Sebastes diploproa						9	+
Engraulis mordax		+	+	9	+		
Eptatretus stoutii		+	+	+	10	10	+
Microgadus proximus	10	+	+	+	+		
Citharichthys stigmaeus			10				+
Dominance and diversity information							
No. tows	15	15	16	15	17	18	16
No. fish	776	1,921	1,161	1,357	2,175	732	1,091
Percent of no. made up by dominant sp.	86	45	25	53	41	38	42
No. spp.	19	25	24	24	34	35	34
Diversity (H_e)	0.70	1.62	2.16	1.66	1.77	2.47	2.00
Number and biomass of fishes captured per square meter[1]							
All species (no./100 m^2)	1.7	4.0	3.0	2.4	4.0	1.4	1.6
(g/m^2)	1.2	2.2	1.4	1.1	2.0	0.9	1.2
(g/m^2 (TS))	1.2	2.3	1.5	1.7	2.4	0.9	2.0
Dover sole (g/10 m^2)	0.2	5.1	3.7	1.4	3.0	2.6	2.8
Rex sole (g/10 m^2)	2.2	3.2	2.0	2.4	2.3	0.2	2.0
Slender sole (g/10 m^2)	<0.1	0.7	0.8	<0.1	5.2	0.8	2.5
Pacific sanddab (g/10 m^2)	9.8	5.8	2.3	6.6	0.6	<0.1	0.4

[1]Based on odometer readings and based on estimates of distance trawled from times and ship's speed (TS).

Pacific sanddab, 37 to 90 m; slender sole, 90 to 183 m; small (≤180 mm TL) rex sole, 55 to 183 m; and small (≤180 mm TL) Dover sole, 55 to 150 m. Therefore the stations sampled in my study were not shallow enough to include all of the major depth range inhabited by Pacific sanddab, rex sole, or Dover sole. Furthermore, large Dover and rex soles are known to be distributed in deeper waters of the upper continental slope off Oregon (Demory 1971; Hosie see footnote 5; Demory[6]), regions unsampled in this study.

The ranks of the dominant species as well as the presence of other species implies a shallow water (74-102 m) and a deepwater (148-195 m) assemblage of fishes. *Cymatogaster aggregata* and *Parophrys vetulus* ranked within the top 10 species at the shallowest Stations 22, 7, 23, and 15 but not at deep Stations 6, 2, and 8 where they were usually absent. *Xeneretmus latifrons* and *Sebastes* juveniles, on the other hand, were only abundant at the deep stations.

Similarity among the stations was calculated as

$$\text{SIMI} = \frac{\sum_{i=1}^{S} P_{1i}P_{2i}}{(Sd_1)(Sd_2)}$$

where S is the number of species present at both stations; P_{1i} is the proportion of the ith species at one station; P_{2i} is the proportion of the ith species at a second station; and $(Sd_1)(Sd_2)$ is the product of the square roots of estimators of Simpson's diversity index for Stations 1 and 2. This measure of similarity was used because it is analogous to a correlation coefficient, relates closely to Simpson's measure of concentration, and has maximum and minimum values of 1 and 0 (McIntire and Moore 1977).

Two assemblages of fishes, a deep and a shallow one, were evident based on high similarity in the species composition among the three deepest stations (2, 6, 8) and among three of the four shallow stations (15, 22, 7) (Table 3). Similarity between stations of each of these two groups varied from 0.85 to 0.95. Station 23, another station at about 100 m (like Stations 7 and 15) also had a fairly high similarity with the other shallow water stations. It was similar to Station 7 (0.92 m) but less similar to Stations 15 and 22 (0.77 and 0.65 m). The benthic environment of Station 23 differed from the other three shallow stations in that it had more than twice the percentage of clay and silt found at Station 22, 7, or 15, where sand was the major sediment component.

TABLE 3.—Indices of similarity (SIMI) for the species composition of fishes among each of the seven stations. Stations are arranged by depth.

	Station					
Station	22	7	15	23	6	2
Shallow:						
22						
7	0.86					
15	0.94	0.93				
23	0.65	0.92	0.77			
Deep:						
6	0.05	0.33	0.14	0.57		
2	0.04	0.26	0.13	0.38	0.85	
8	0.18	0.45	0.29	0.58	0.91	0.95

Based on sediment composition two of the three station pairs were very similar (Table 3): Stations 22 and 15 (SIMI = 0.94), and Stations 6 and 8 (SIMI = 0.91). Stations 7 and 2, another station pair, at 100 and 190 m, had a similarity of only 0.26. This disparity may be explained by the thin layer of silt overlying a predominantly sandy sediment at Station 2. For epifaunal organisms the sediment type at this station may have been more similar to that at Stations 6 and 8 than any other stations. This may explain why Station 2 is so similar in species composition to Stations 6 and 8. However Station 7 showed high similarity (0.92-0.93) with Stations 15 and 23, stations with different sediment types but both at the same depth. Thus clear separation of the effects of depth and sediment was not always possible. Nevertheless the most consistent and obvious assemblages were correlated with depth. Stations of different sediment types had high similarity within the shallow water assemblage.

These results agree with those of Day and Pearcy (1968) who studied the distribution of demersal fishes from 40 to 1,829 m along a transect just north of Heceta Bank. They delineated a species association at depths of 42-73 m on sandy sediments with Pacific sanddab as the dominant species and an association at 119-199 m on silty-sand sediments where slender sole predominated. Because the same species associations sometimes were found on different sediment types, they felt that factors other than sediment texture may govern the distribution of fish assemblages.

Diversity

The number of species of fishes collected was

[6]Demory, R. L. 1975. The Dover sole. Oreg. Dep. Fish Wildl. Inf. Rep. 75-4, 4 p.

highest (34-35) at the deep stations, intermediate (24-25) at the 100-m stations and lowest (19) at the shallow station (Table 2B). Species diversity calculated by the information function (Shannon and Weaver 1963):

$$H_e = -\Sigma_{pi} \ln_{pi}$$

varied between 0.7 and 2.5 at the seven stations. Diversity was lowest at the shallow, sand station where sanddab composed 86% of the catch. Diversity was highest at Station 2, which had the largest number of species, and next highest at Station 23, where the dominant species composed only 23% of the total number of fishes. Since the number of species was similar among the three 100-102 m stations or the three deep (148-195 m) stations, differences in diversity within these two groups are due to variations in the evenness of the proportions of the various species.

The values of diversity are similar to those found by others for demersal fish communities. Margalef (1968) reported that diversity (H) of bottom fishes trawled off the Spanish Mediterranean ranged from 1.0 to 2.4. Haedrich and Haedrich (1974) calculated H = 0.7-1.7 for demersal fishes of Block Island Sound [from the data of Merriman and Warfel (1948) and Richards (1963)], and H = 1.6-1.8 for bottom fishes on the continental slope off southern New England. Haedrich et al. (1975) give a value for H of 1.9 for 141-285 m on the continental slope south of New England.

Biomass Estimates

Based on odometer estimates of distance trawled, numbers varied from 1.4 to 4.0/100 m^2, and biomass ranged from 0.9 to 2.2 g m^{-2} (Table 2). Estimates of the biomass of fishes based on ships's speed (3,700 m h^{-1}), average trawling times on the bottom (16 min) and the width of the beam trawl are in agreement with the estimates that used odometer readings.

The biomass of the four common flatfishes at each station shows that the Pacific sanddab composed nearly all the biomass at Station 22 and also had the largest biomass at Stations 7 and 15. Dover sole predominated in catches at Stations 23, 2, and 8, and slender sole was the dominant fish at Station 6. These trends are similar to those noted earlier for species numbers (Table 2).

Catches of demersal fishes with the small beam trawl at these seven stations are low compared with other estimates made with commercial-sized otter trawls off Oregon and Washington. On the basis of surveys using an otter trawl with a 23-m footrope with 9.9-cm mesh (estimated to have a 9-m horizontal and a 1.5-m vertical mouth opening), Demory and Hosie[7] calculated that the average biomass of fishes on the continental shelf of Oregon was 19 g m^{-2} in 1971-72 and 16 g m^{-2} in 1973-74. Barss et al.[8] employed similar methods to estimate a standing stock of trawlable fishes on the continental shelf and upper slope (18-549 m) of Washington of about 15 g m^{-2}. In both of these studies, a large portion of the catch consisted of rockfishes, *Sebastes* spp., Pacific hake, *Merluccius productus*, other roundfishes, skates, and other elasmobranchs. The average biomass of flatfishes, the type of fishes that their trawl was designed to catch, was 5.7 and 5.4 g m^{-2} for 1971-72 and 1973-74, respectively, off Oregon and 9.0 and 7.5 g m^{-2} for 1975 and 1976 off Washington. Alverson et al. (1964), also using large otter trawls (28-m footrope) with large (11-cm) mesh, provided data from which a biomass of 8.0 g m^{-2} for demersal fish and 3.1 g m^{-2} for flatfishes can be estimated for the continental shelf of Oregon and Washington. Our estimates are also low compared with the values given by Oviatt and Nixon (1973) for New England waters.

Although all these values are approximations dependent on the accuracy of estimates of actual distance trawled and the effective mouth area, the otter trawl catches are several times larger than my beam trawl estimates. Nektobenthic fishes, such as hake and rockfishes, as well as large demersal flatfishes and skates are poorly sampled with the beam trawl because they are not available to the net or they avoid the trawl (see also Day and Pearcy 1968). Thus, retention of small species of fishes and juveniles of large species by the beam trawl, fishes that may escape through the meshes of the larger nets, do not compensate for fishes that avoid the beam trawl or nektobenthic species that range above the bottom.

Kuipers (1975) estimated that the catch efficiency of a 2-m beam trawl decreased exponentially with increasing length of plaice, *Pleuronectes platessa*, from approximately 100%

[7]Demory, R. L., and M. J. Hosie. 1975. Resource surveys on the continental shelf of Oregon. Fish Comm. Oreg., Annu. Rep., 9 p.

[8]Barss, W. H., R. L. Demory, and N. Ten Eyck. 1977. Marine resource surveys on the continental shelf and upper slope off Washington, 1975-76. Oreg. Dep. Fish Wildl. Rep., 34 p.

for plaice under 7 cm to 15-30% for plaice over 15 cm. Riley and Corlett (1965) and Edwards and Steele (1968) estimated catch efficiencies of 57% and <45% for 0-group plaice in 2-m and 4-m beam trawls, respectively. In this study, the 3-m beam trawl caught about one-fourth the biomass of flatfishes per square meter caught by Demory and Hosie (see footnote 7) off Oregon, indicating a low catch efficiency.

The length-frequency distributions of Pacific sanddab and rex sole caught in the beam trawl are compared in Figure 2 with those caught in two larger otter trawls with large-sized mesh by Demory and Robinson[9] off Oregon. The small-meshed beam trawl retained appreciably smaller individuals than the otter trawls, verifying that it was most effective in capturing small flatfishes and that large fishes effectively avoided this small net.

The disparity between the estimates of abundance by otter trawls and the beam trawl may be magnified by the effects of otter doors, bridles, and towing cables. The bridles from the otter doors to the net (sweeplines and dandy lines) in combination with the wake from the doors can herd fishes into the net from a wide area in front of the trawl, thereby increasing the effective mouth opening (Loverich[10]). Thus the abundance estimates cited above that are based on the horizontal spread of otter trawl nets are probably too large. The towing cable of the beam trawl, on the other hand, drags on the bottom immediately in front of the trawl and therefore may frighten fishes away from the net tow path. Size-dependent responses of fishes to the bottom disturbances created by trawl doors, bridles, and cables may contribute to the differences found in size of fishes captured by the two types of trawls. Large fishes, with better swimming capabilities, may be herded more effectively by otter trawl bridles than small fishes. Large fishes may also rapidly swim away from the towing cable of the beam trawl.

[9]Demory, R. L., and J. G. Robinson. 1973. Resource surveys on the continental shelf off Oregon. Fish. Comm. Oreg., Annu. Rep., 18 p.

[10]Loverich, G. 1975. Trawl nets evaluated by expert. Fisherman's News, Sept. 1975 and pers. commun.

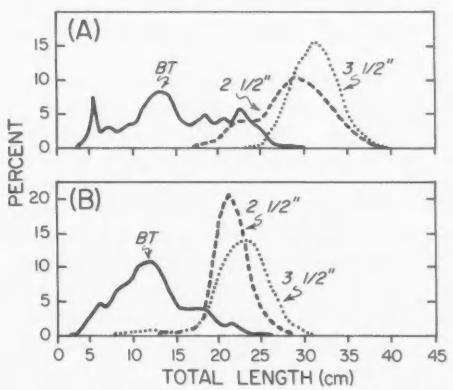

FIGURE 2.—Comparison of length-frequency distributions of (A) rex sole and (B) Pacific sanddab captured in the beam trawl (BT) with 13-mm mesh with those captured by Demory and Robinson (see footnote 9) in 3½-in (89-mm) mesh and 2½-in (64-mm) mesh otter trawls on the continental shelf off Oregon in 1971 and 1972.

Environmental Effects

An analysis of variance, using a linear model with depth as a continuous variable and sediment, season, and year as indicator variables, was completed on the untransformed data for numbers and weight of fishes per square meter and numbers and weight per tow. Sediment was classified as four types based on the percent of sand (2-4, 28, 63-69, 84-99%). Trawls were combined into two seasons, October-April (winter), and May-September (summer). Levels of significance, $P<0.05$ and $P<0.01$, are shown in Table 4. Because of the large number of tests, only effects with $P<0.01$ are considered significant, although $P<0.05$ are shown to provide indications of possible trends. Effects with $P<0.05$ will only be discussed if they reinforce an effect of $P<0.01$, or if two effects of $P<0.05$ were found in the same species-effect category.

Sediment Effects

The number and biomass of slender sole caught per tow appeared to be affected by sediment type (Table 4). This is curious because this species is primarily a pelagic feeder (Pearcy and Hancock 1978). Largest catches per tow were made at stations with high percentages of clay and silt, and lowest catches occurred on sandy sediments. Based on sediment types (and stations), catches of slender sole ranked as follows: 2-3% sand (6-8) >63-69% sand (2-7) >28% sand (23) >84-99% sand (22-15) (see also Table 2). The same trend with sediments is indicated ($P<0.05$) for slender sole weight per square meter, but because catches per square meter were more variable or mean differences were less, differences were not significant at $P<0.01$.

TABLE 4.—Results of an analysis of variance (ANOVA) of the numbers and weights of fishes caught per square meter or per tow[1]; * indicates $P<0.05$; ** $P<0.01$. R^2 (coefficients of determination) values are given below.

		All species				Rex sole				Dover sole				Slender sole				Pacific sanddab			
		No.		Wt.		No.		Wt.		No.		Wt.		No.		Wt.		No.		Wt.	
Item	df	m^2	Tow	m^2	Tow	m^2	Tow	m^2	Tow	m^2	Tow	m^2	Tow	m^2	Tow	m^2	Tow	m^2	Tow	m^2	Tow
Year	2	**	**	**	**	**	*	**		**		**		*	*	*		**		**	
Sediments	3					*							*		**	*	**			*	*
Seasons	1													*							*
Sediment × season	3						*					*			*	*					
Depth	1		*		*			*	*									*	**	*	**
Depth × season	1	**		**		**	*	*		**	*									*	*
Error	95																				
Total	106																				
R^2 (tow)			0.18		0.20		0.23		0.16		0.17		0.16		0.36		0.33		0.28		0.34
R^2 (m^2)			0.39		0.51		0.47		0.40		0.46		0.43		0.24		0.28		0.36		0.37

[1]An ANOVA using a square root transformation for the data on all species combined per tow and per square meter gave similar significance effects. The ANOVA was unbalanced because of unequal numbers of observations per station, season, depth, etc. Effects were tested using the extra sum of squares principle (Searle 1971).

The biomass of Pacific sanddab, on the other hand, showed opposite trends ($P<0.05$) and was large on sandy sediments and small on silt or clay sediments (see also Day and Pearcy 1968; Barss et al. see footnote 8). Since the effect of sediment was not significant for total fish catch by numbers or weight sandy stations with low percent organic carbon, apparently did not support a markedly lower abundance of demersal fishes (Table 2). Although adult Dover sole show a strong preference for mud or silt bottom (Barss et al. see footnote 8; Demory see footnote 6), this trend was not apparent for the small Dover sole caught inshore of Heceta Bank in this study.

A sediment-season effect was indicated for slender sole. They were caught in larger numbers per tow and weight per square meter ($P<0.05$) at the stations with a low percentage of sand (6-8) in the winter than the summer.

Depth Effects

The slope of the regression between depth and number and weight per tow of Pacific sanddab was significant ($P<0.01$) and negative. Catches per square meter on a number and weight basis gave the same trends ($P<0.05$). Sanddab were most abundant in shallow water. Weight of rex sole per square meter and per tow and total fish numbers and weight per tow also tended to decrease ($P<0.05$) with depth.

Depth-season interactions were significant on a square meter basis for all species combined (number and weight) and for numbers of rex and Dover soles. These effects were caused by appreciably larger catches in deep water in winter than summer. Seasonal differences were small in shallow water. This trend for lower catches on the outer edge of the continental shelf during summer than winter was obvious for Pacific sanddab. They were completely absent from the deep stations (2, 6, 8) during the summer but were present at all stations during winter. Seasonal bathymetric migrations, with spawning migrations into deep water in the winter and return to relatively shallow depths in the summer, have been described for Dover sole and rex sole by Hagerman (1952), Harry (1956), Alverson (1960), and Demory (1971). Such movements could explain these depth-season effects.

Seasons

No significant seasonal differences were detected, indicating little seasonal variation in catches of these species when all stations are combined.

Year Effect

On the basis of numbers and weight per square meter and per tow, more fishes were captured in 1969 and 1968 than in 1970 at all stations (Figure 3). This trend was significant ($P<0.01$) for all species combined and for rex sole, Dover sole, and Pacific sanddab. Year effects were also indicated for slender sole ($P<0.05$). I have no cogent explanation for these large annual variations. They could represent actual variations in abundance or availability, due to natural events or increased fishing activity, or to undetected changes in sampling efficiency. Dominant year classes have been reported for these flatfishes off Oregon (Demory and Robinson see footnote 9), which may contribute to these annual differences, though changes in length-frequency distributions were not obvious over this 2-yr period.

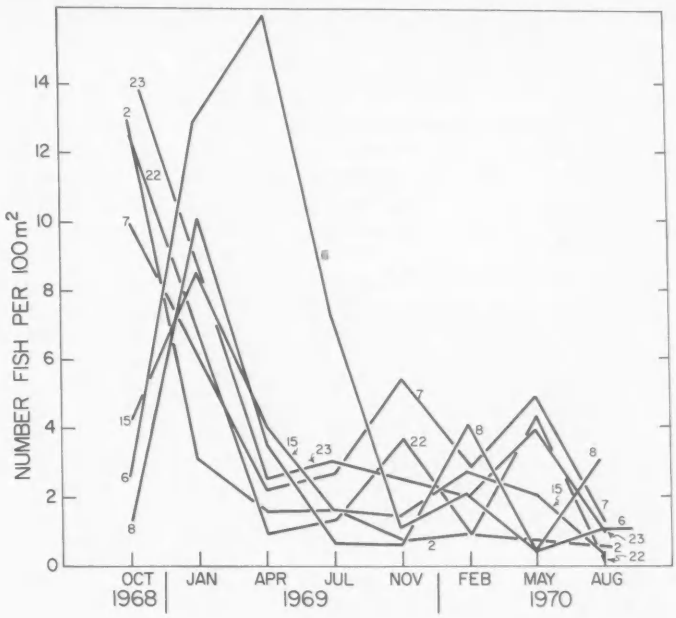

FIGURE 3.—Variations in the total numbers of fishes caught at each of the seven stations, 1968-71. The two tows at each station for each sampling period were averaged.

The amount of variability explained by the regression (R^2) of all effects on catches ranged from 0.16 to 0.51 (Table 4). Values were larger for the analysis based on catches per square meter than catches per tow, except for slender sole. These low values indicate that most of the variability was not accounted for by the variables of sediment, depth, year, and season. Large residual mean squares indicate that sampling variability associated with catches at individual stations is appreciable. Oviatt and Nixon (1973) completed a multiple regression analysis of biomass and numbers of benthic fishes in Narragansett Bay, R.I., with 14 environmental variables. Depth and sediment organic content contributed significantly to the regression for total fish numbers and fish biomass. But an R^2 of only 0.21 was found. In both of these studies, only a small fraction of the total variability was explained by the environmental factors included.

Size-Frequency Distributions

Differences in length-frequency distributions were sometimes obvious among the stations located at different depths or sediment types. For example, the main length mode of rex sole at the 100- and 102-m stations was 125 mm, but at 190- and 195-m depth there was a distinct bimodal distribution with peaks at 45 and 215 mm (Figure 4). These differences imply that young-of-the-year

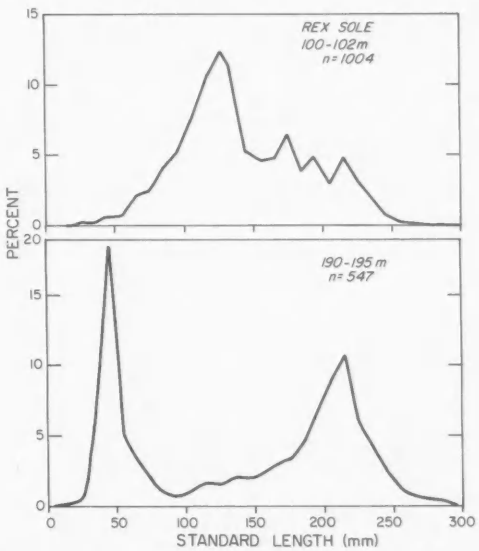

FIGURE 4.—Length-frequency data for rex sole at 100-102 m stations (above) and 190-195 m stations (below).

(<50 mm) and age-groups III-V (200-250 mm) rex sole (see Hosie and Horton 1977 for age-length data) preferentially inhabit deep waters on the outer edge of the continental shelf while intermediate sizes (75-150 mm) inhabit shallower waters of the inner shelf. The peak of young-of-the-year rex sole at 200 m corroborates the conclusion of Pearcy et al. (1977) about the depth of larval settlement and the nursery ground for early benthic life. They concluded that rex sole larvae settle to the bottom mainly on the outer continental shelf during the winter when they are >50 mm SL. Powles and Kohler (1970) and Markle (1975) believed that the nursery grounds of *Glyptocephalus cynoglossus* are also in deep waters off the east coast of the United States.

Small Pacific sanddab (<70 mm) composed a larger proportion of the catch at 102 m where sand was 28% of the sediment (Station 23) than at 74 and 102 m where sand made up over 64% of the sediment (Stations 22, 15) (Figure 5). Young sanddab appear to inhabit deeper water with finer sediments in early life and then aggregate on sandy bottom areas in shallow water where they often dominate the demersal fish fauna. Hence, this trend of decreasing depth with increasing age is similar to that found for rex sole.

SUMMARY

1. Demersal fishes were sampled at seven stations on Oregon's central continental shelf at various seasons of the year during a 2-yr period. A fine-meshed, 3-m beam trawl was used in order to quantitatively sample small flatfishes. The stations ranged from 74 to 195 m deep and had sediment types ranging from nearly 100% sand to clayey-silts with about 3% sand.

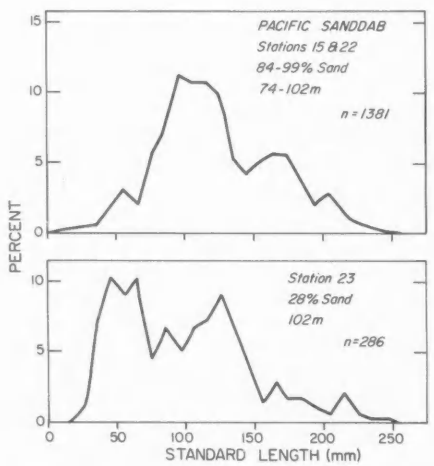

FIGURE 5.—Length-frequency data for Pacific sanddab at stations with 84-99% sand (above) and 28% sand (below).

2. Stations were selected in an attempt to separate the effects of depth and sediment on the assemblages of fishes and abundances of common species. Three station-pairs were recognized that had similar sediment types but were located at different depths. Separation of sediment and depth effects was complicated however by differences in measured (and possibly unmeasured) factors between station pairs.

3. Two general assemblages of fishes were recognized on the basis of species composition of fishes by numbers, biomass per square meter of dominant species, and similarity indices among the seven stations. These were a shallow water (74-102 m) assemblage dominated numerically by Pacific sanddab, and a deepwater (148-195 m) assemblage dominated by slender sole.

4. Species diversity (H) varied between 1.6 and 2.5 except at the shallow, sand station where it was only 0.7. Dominance was pronounced at this station: 86% of all the individual fishes captured were Pacific sanddab. The largest number of species (34 or 35) was recorded for the three deep stations. These values of H are similar to others for temperate, demersal fish communities.

5. Similarity indices of the species composition of fishes were high for two of the three station pairs with similar sediments. However, indices were also high among the four shallow stations of differing sediment types. Stations that were near each other geographically were similar, indicating the possibility of a proximity effect, but high similarity was also found among deep stations, one of which was over 65 km from the others.

6. An analysis of variance of the number and weight per square meter and per tow of Dover, rex, and slender soles, Pacific sanddab, and all species combined indicates some effects of sediments and depth. Largest catches of slender sole were at the clayey-silt station pair, and largest catches of Pacific sanddab were on sandy sediments. Catches of Pacific sanddab were significantly larger at the shallow stations. Catches of rex sole and all species combined also tended to decrease with increasing depth.

7. Differences in the length-frequency distributions of Pacific sanddab and rex sole were corre-

lated with depth or sediment type. Small sanddab predominated on the silty-sand station, whereas large sanddab preferred sandy sediments. Young-of-the-year rex sole were concentrated on the outer edge of the continental shelf (190-195 m).

8. Catches were sometimes larger in the winter than the summer, especially at the deep stations. This trend, which was noted for all four flatfishes and for all species combined, is probably the result of seasonal bathymetric movements.

9. A pronounced decrease in the catches of most species and total catch per square meter occurred during the 2 yr of this study. Reasons for this decline are unknown.

10. The biomass of benthic fishes ranged from 0.9 to 2.4 g m^{-2} at the seven stations. Biomass was not appreciably lower at the pure sand stations, which had about 0.1% organic carbon in the sediment. This is related to the fact that the Pacific sanddab, the predominant species at this station, is a pelagic feeder (see Pearcy and Hancock 1978).

11. The weight of fishes per square meter caught in the 3-m beam trawl was several times lower than that estimated from larger otter trawls with coarser meshes. Although the beam trawl caught many small flatfishes, large fishes and nektobenthic species effectively avoided this small beam trawl, resulting in low biomass estimates.

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FEEDING HABITS OF DOVER SOLE, *MICROSTOMUS PACIFICUS*; REX SOLE, *GLYPTOCEPHALUS ZACHIRUS*; SLENDER SOLE, *LYOPSETTA EXILIS*; AND PACIFIC SANDDAB, *CITHARICHTHYS SORDIDUS*, IN A REGION OF DIVERSE SEDIMENTS AND BATHYMETRY OFF OREGON

WILLIAM G. PEARCY AND DANIL HANCOCK[1]

ABSTRACT

The feeding habits of the Dover sole and rex sole (mainly juveniles) and of slender sole and Pacific sanddab were investigated at seven stations on the continental shelf off central Oregon. Dover sole had a catholic diet, feeding on a large variety of infaunal and epifaunal invertebrates. The composition of the diet varied among stations of different depth and sediment type indicating opportunistic feeding. Pelecypoda were the most important prey on a weight basis at the shallow station (74 m) of well-sorted sand where they were the dominant macrofaunal invertebrate. Ophiuroids, sea pens, anemones, and pelecypods were the most important prey at 100-102 m stations of silty sand or sandy silt. Polychaetes composed over 90% of the diet at the deep stations (148-195 m) of clayey silt or silty sand. The average standing stocks per square meter of Dover sole caught in beam trawl collections and polychaetes in grab samples were positively correlated among stations.

Similarity of the food habits of Dover sole on the basis of food weight or frequency of occurrence was generally higher among stations of similar depth than of similar sediment texture. Similar trends were noted for assemblages of benthic fishes and invertebrates.

Dover sole collected during the winter had the highest percentage of empty stomachs, the fewest prey taxa, and often the lowest frequency of occurrence of prey taxa within a size group. Because seasonal variations were not observed in abundance of macrofaunal food in the sediments, availability of prey may change with season, or more likely, Dover sole feed more intensely and less selectively during summer.

Small (<150 mm standard length) rex sole fed mainly in amphipods and other crustaceans. Large (150-450 mm standard length) rex sole preyed chiefly on polychaetes. The diet of rex sole was less diverse than that of the Dover sole and overlap of diet between the two species was not large.

Both the Pacific sanddab, numerically the most common species of fish at the shallow sand station, and the slender sole, the most common species at the three deep, soft-sediment stations, preyed principally on pelagic crustaceans such as euphausiids, shrimps, and amphipods. Although the biomass of mollusks in the sediments was large at the shallow sand station, they were not consumed by Pacific sanddab. Fish were occasionally an important food for the sanddab.

The objectives of this study were: 1) to describe the food habits of the four species of flatfishes that are common in trawl catches on the central continental shelf off Oregon: Dover sole, *Microstomus pacificus*, rex sole, *Glyptocephalus zachirus*, slender sole, *Lyopsetta exilis*, and Pacific sanddab, *Citharichthys sordidus*; 2) to evaluate the possible effects of depth and sediment, size of fish, and season of capture on their food habits; and 3) to compare the biomass and composition of fish food from grab samples with feeding habits of fishes.

These species are among the most abundant flatfishes in demersal communities of this region of the Pacific Ocean (Alverson et al. 1964; Day and Pearcy 1968; Alton 1972; Demory and Hosie[2]). They dominated the fish catches at the stations where they were captured for this study (Pearcy 1978). In order to know more about the role of these fishes in their ecological communities, including competitive-predatory relationships, more data are required on their food habits.

Hagerman (1952) listed food items found in Dover sole caught in California waters. Pearcy and Vanderploeg (1973) listed general taxonomic groups preyed upon by Dover, rex, and slender soles and Pacific sanddab. Kravitz et al. (1977) gave a detailed account, including species of prey

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[2]Demory, R. L., and M. J. Hosie. 1975. Resource surveys on the continental shelf of Oregon. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Commer. Fish. Res. Dev. Act, Annu. Rep. July 1, 1974 to June 30, 1975, 9 p.

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consumed by the rex sole and Pacific sanddab caught in a single collection off the central Oregon shelf. This study is, to our knowledge, the most complete study of the food habits of these four species.

METHODS

Fishes were collected during 115 tows with a 3-m beam trawl at seven stations on the continental shelf off central Oregon between August 1968 and August 1970. These stations are classified by four depth categories and the percentage of sand in the sediments in Figure 1. Details on methods and descriptions of the stations are given by Pearcy (1978).

All fishes were preserved at time of capture with Formalin,[3] and the body wall of large (>150-200 mm SL) fishes was incised to insure preservation of stomach contents. Fishes were identified and measured (standard length, SL) in the shore laboratory. Stomachs were removed from 326 Dover sole represented in the catches at all seven stations; and from 614 rex sole, 1,109 slender sole, and 723 Pacific sanddab captured at two or three stations where each of these species was most common.

Stomach contents were removed and empty stomachs were noted. Food organisms were identified to species when possible. Annelids, crustaceans, mollusks, echinoderms, coelenterates, and remaining taxa (major taxa) were weighed to the nearest 0.01 g (wet-preserved weight). Usually these weights were obtained for the contents of a single stomach, but when the contents were insufficient for accurate weighing, taxa from the stomach contents of several fish of the same species and size, and from the same tow, were combined and weighed together to constitute an observation. The number of observations for Dover, rex, and slender sole and Pacific sanddab were 325, 374, 607, and 392, respectively.

Results are reported as the a) percent that each major food taxa constitutes of the total wet weight of food found in stomachs for all seasons combined and for winter and summer seasons separately; and b) the frequency of occurrence (FO) of principal prey, i.e., species or taxa found in 5% or more of the observations for a species or size group of a species for all seasons combined.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

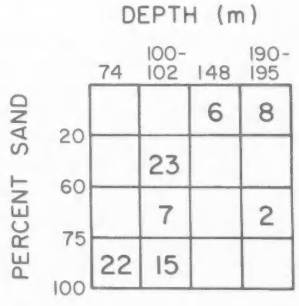

FIGURE 1.—Classification of the seven stations, each indicated by station number, according to depth of water and percent of sand (0-20, 20-60, 60-75, and 75-100%). The stations with similar sediment types but different depths are 6 and 8, 7 and 2, and 22 and 15. (See Pearcy 1978 for additional information.)

RESULTS

General Food Habits

Two general feeding types are indicated by differences in the weights of major food taxa (annelids, crustaceans, mollusks, echinoderms, coelenterates, and other taxa) found in the stomach contents of the four species (Table 1). Dover and rex soles fed largely (64%) on annelids, while slender sole and Pacific sanddab fed mainly on crustaceans (75%). Within these two apparent feeding types, differences occurred among the proportions of prey taxa of secondary importance. For example, crustaceans were more abundant in the diet of rex than Dover sole (31% vs. 11%), whereas mollusks were more abundant in Dover than in rex sole (18% vs. 1%). Annelids composed more of the stomach contents of slender sole than Pacific sanddab (15% vs. 7%).

Based on the average frequency of occurrence of principal prey (FO≥5%) from all sizes of fish and from all stations (Table 2), it is obvious that the food habits within these two feeding types (Dover sole-rex sole vs. slender sole-Pacific sanddab) are not as similar as shown by Table 1. Principal prey of Dover sole, for example, included 11 different identified polychaetes. Rex sole preyed mainly on three identified species of polychaetes. Only one principal prey species of polychaete was common to the diet of both Dover and rex soles. The shrimp *Pandalus jordani*, pelecypods, and ophiuroids were principal prey in the food of Dover but not rex sole, whereas crab larvae, cumaceans, and *Oiko-*

TABLE 1.—Percent by weight that major food taxa composed of the diet of the four flatfishes, all stations and seasons combined.

Taxa	Dover sole	Rex sole	Slender sole	Pacific sanddab
Annelida	64.4	64.8	15.6	7.2
Crustacea	11.2	31.0	75.6	74.8
Mollusks	18.3	1.4	0.7	0
Echinoderms	3.4	<0.1	<0.1	0
Coelenterates	2.6	0	0	0
Other taxa	0	2.8	8.2	18.0

TABLE 2.—Average frequency of occurrence of principal prey (those occurring in 5% or more of the observations) in the four species, all stations combined.

Prey	Rex sole	Dover sole	Slender sole	Pacific sanddab
Polychaeta:				
Sternaspis fossor	12	14		
Myriochele heeri		15		
Nothria geophiliformis	9			
Goniada brunnea	10			
Aricidea neoseucica		6		
Haploscoloplos elongatus		9		
Chaetozone setosa		6		
Terebellides stroemii		6		
Rhodine bitorquata		5		
Typosyllis hyalina		9		
Lumbrineris sp.		6		
Amphicteis sp.		5		
Glyceridae		5		
Unidentified	25	19	7	
Crustacea:				
Pandalus jordani		6	7	
Euphausia pacifica			9	7
Crab larvae or juvenile	7			13
Gammarid amphipods	29	24		
Copepods				12
Cumaceans	8			
Unidentified	16	12	21	24
Mollusca:				
Pelecypoda		12		
Echinodermata:				
Ophiuroidea		12		
Miscellaneous:				
Oikopleura spp.	7			
No. observations	347	325	607	392
No. fish	614	326	1,109	723

pleura were principal prey of rex but not Dover sole. Gammarid amphipods occurred frequently in stomachs of both rex and Dover soles; had they been identified to species, the overlap between the diets of the Dover and rex soles would appear even smaller. Overlap in the diets of Dover and rex soles of various size groups were also found to be small.

Gammarid amphipods, the major crustacean prey of Dover and rex soles, were not principal prey for slender sole and Pacific sanddab. Slender sole and Pacific sanddab fed largely on pelagic crustaceans, as indicated by the occurrence of euphausiids in stomachs of both species, by crab larvae and calanoid copepods in sanddab, and by *Pandalus jordani* in slender sole. Slender sole and Pacific sanddab are chiefly pelagic feeders. *Pandalus jordani* is known to migrate off the bottom at night (Pearcy 1970) and hence could have been consumed on the bottom or in midwater by slender sole. We have occasionally caught both slender sole and Pacific sanddab in midwater trawls at night. Barss[4] caught in midwater trawls at night Pacific sanddab that had been feeding heavily on northern anchovy, *Engraulis mordax*. The only good evidence for benthic feeding by either of these two species is the presence of annelids in their diets (Table 1).

Differences Among Stations

The proportions (by weight) of the major taxa in the diet of Dover sole were sometimes markedly different among stations (Table 3). Prey composition and availability may be functions of sediment and/or depth. Annelids constituted over 90% of the diet on a weight basis at the three deepest stations (2, 6, and 8), but <13% at the shallowest station (22) where the sediment was well-sorted sand. At this shallow station, mollusks and crustaceans were the major food items in the diet. Coelenterates (feeding polyps of sea pens and anemones) and echinoderms (brittlestars) were minor food taxa for Dover sole at all stations except Stations 15 and 23 (102 m depth), where together they composed over one-half the diet. The proportion of fish with food in their stomachs was also higher at these two stations than at any of the other stations.

To illustrate the similarities of the food habits of Dover sole among these stations, we constructed a station-station matrix (Table 4) using an index (C_λ) that Horn (1966) recommended for comparing overlap in exploitation of alternative food sources

[4]Barss, W. H. (compiler). 1976. The Pacific sanddab. Oreg. Dep. Fish Wildl., Inf. Rep. 76-5, 5 p.

TABLE 3.—The average percentage composition of stomach contents of Dover sole on a weight basis at each of the stations.

	Station (depth in meters in parentheses)						
Taxa	22 (74)	7 (100)	15 (102)	23 (102)	6 (148)	2 (190)	8 (195)
Annelids	12.6	59.9	25.0	30.5	91.9	93.4	91.0
Crustaceans	29.6	14.1	3.3	3.1	3.7	3.5	6.5
Mollusks	57.9	23.7	13.5	12.4	3.0	2.2	0.3
Echinoderms	0	1.1	33.8	30.1	1.4	1.1	2.2
Coelenterates	0	1.2	24.3	23.8	0	0	0
Other taxa	0	0	0	0.1	0	0	0
No. fish examined	65	38	22	10	49	91	51
No. fish with stomach contents	28	19	20	10	22	61	32

TABLE 4.—Similarity (C_λ) in the diets of Dover sole at the seven stations based on the percentage of major taxa in their diets on a weight basis (below diagonal) and frequency of occurrence of principal polychaete prey (above diagonal). Stations are arranged by depth.

	Frequency of occurrence						
Stations	22	7	15	23	6	2	8
22		0.04	0	0	0.09	0.06	0
7	0.58		0.64	0.57	0.24	0.54	0.05
15	0.34	0.56		0.59	0.21	0.38	0
23	0.34	0.64	0.99		0.09	0.42	0
6	0.22	0.88	0.44	0.52		0.37	0.42
2	0.21	0.87	0.43	0.52	1.00		0.45
8	0.21	0.88	0.43	0.53	1.00	1.00	

within the same habitat. This measure of similarity varies from 0 to 1.0. The percentages by weight of the major taxa (lower half of Table 4) were identical at the three deepest (148-200 m) Stations: 2, 6, and 8. Stations 15 and 23, both located at 102 m depth, were also very similar. Station 7 at 100 m was fairly similar ($C_\lambda > 0.87$) to Stations 2, 6, and 8 located in deeper water. The percent of major taxa in the diet of Dover sole at the shallow, sand location (Station 22) was not very similar to any other station ($C_\lambda \leq 0.58$).

The frequency of occurrence of principal prey of Dover sole (Table 5) indicates fairly low similarity among different stations for species of polychaetes. Most species occurred at only one or two stations and the assemblage of polychaetes eaten by Dover sole appears to be different at each station. As one would expect, similarity is higher when higher taxa such as gammarid amphipods or pelecypods are considered as a group. For this reason comparisons of similarity among stations should be confined to prey identified to the same taxonomic level.

To examine differences in prey species among stations we calculated the overlap in diet (C_λ) based on polychaetes alone, the most common and speciose prey animals of Dover sole (and the food group that one of us (Hancock) was familiar with taxonomically). The range in overlap of diets based on frequency of occurrence of individual taxa of polychaetes at these stations (Table 5) was appreciably lower than that based on weight percentage of major taxa (upper half of Table 4). Stations 2, 6, and 8, which were very similar on the basis of the weight of major taxa in the Dover sole stomachs, overlapped only moderately on the basis of frequency of occurrence of polychaetes ($C_\lambda = 0.37 - 0.45$). Stations 15 and 23, similarly based on major taxa, were the most similar ($C_\lambda = 0.64$) stations based on frequency of occurrence of polychaetes. Station 23 was the next highest in similarity with Stations 7 and 15. Thus, the polychaete prey of Dover sole were most similar among these three 100-102 m stations.

TABLE 5.—Frequency of occurrence of principal prey of Dover sole from the seven stations.

Taxa	Stn 22	7	23	15	6	2	8
Polychaeta:							
Sternaspis fossor		23	24	6		32	
Myriochele heeri		31	14	6	8	27	
Nothria geophiliformis					9	14	13
Chloeia pinnata						36	16
Melinna cristata						14	
Goniada brunnea		7			8	14	
Aricidea uschakowi		5			9		
Aricidea neosuecica		9			23		
Haploscoloplos leongatus					25	18	8
Owenia fusiformis		10				18	
Maldane sarsi		5	6				
Chaetozone setosa		8		6	8	9	
Terebellides stromenii		11	10				
Tharyx multifilis					6		8
Rhodine bitorquata		13					
Typosyllis hyalina		25		6			
Ammontrypane aulogaster							5
Nephtys cornuta							11
Anaitides groenlandica	10						
Lumbrineris sp.		12			6		
Ammontrypane spp.						9	
Amphitteis		9				18	
Aricidea spp.							5
Pherusa papillata		7					
Tharyx spp.					9		
Nephtys spp.		5		8		8	
Terebellidae						9	
Ampharetidae							5
Maldanidae						9	
Lumbrineridae					11		
Glyceridae		10	8				
Spinonidae	10	5			6	9	
Hemipodus borealis	10						
Laonice cirrata		6					
Megelona sp.		5					
Crustacea:							
Pandalus jordani	30	7	16			23	8
gammarid amphipod	70	22	22	24	14	45	26
copepod	20						
cumacean		7					8
Diastylis spp.							8
Valvifera spp.	10						
Ostracoda	10					14	5
unidentified crustacea							
Mollusca:							
Gastropoda		7					
Solenogasters spp.		7					8
Pelecypoda	20	20		10	16		8
Yoldia ensifera			8				
Lucina sp.						9	
Megacrenella columbiana		10		10			
Tellina salmonea	10						
Acila castrensis	10						
Echinodermata:							
Ophiuroidea		11	27	16		23	
sea pen			12				
Miscellaneous:							
Nematoda						18	
No. observations	10	91	51	49	64	22	38
No. fish	10	91	51	49	65	22	38

Because stomachs of the other flounders were examined for only two or three stations, few station comparisons could be made. As with Dover sole, the percentage of major taxa in the diets of rex sole at Stations 2, 6, and 7 were similar, and food habits were almost identical at Stations 2 and

TABLE 6.—The average percent by weight that major taxa composed of the diet of rex sole, slender sole, and Pacific sanddab at Stations 7, 6, and 2.

	Rex sole			Slender sole			Pacific sanddab	
Taxa	Stn 7	6	2	7	6	2	7	6
Annelida	58.7	69.7	64.5	1.2	18.5	13.1	8.2	0.1
Crustaceans	39.2	24.8	29.6	92.2	72.3	77.8	71.3	99.9
Mollusks	2.1	1.0	0.5	0.9	0.8	0	0	0
Echinoderms	0	0	0	0	0	0	0	0
Coelenterates	0	0	0	0	0	0	0	0
Other taxa	0	4.5	5.5	5.8	8.5	9.1	20.5	0
No. fish examined	376	210	28	68	844	197	690	33
No. fish with stomach contents	262	160	25	35	403	83	478	13

6 (Table 6). A larger percentage of crustaceans (and the lowest percentage of annelids) was found at Station 7 than at 2 or 6 for both rex and slender soles. But crustaceans were more abundant in the diet of sanddab at Station 6 than at Station 7. Fishes (included as other taxa) were an appreciable part of the sanddab diet at Station 7. Again, differences in availability of food taxa apparently occurred among stations for the same predator species, and different trends in the importance of food taxa are evident for different species of fish at the same stations.

The principal prey were most similar for rex sole at Stations 2 and 6, as were the major taxa by weight. The polychaete *Nothria geophiliformis* and the larvacean *Oikopleura* occurred in over 5% of the observations only at these two stations. It is curious that the planktonic *Oikopleura* was so frequent in the diet of this primarily benthophagus fish. Other prey common at all these stations included the polychaete *Goniada brunnea*, unidentified polychaetes, gammarid amphipods, and cumaceans.

Pandalus jordani was a principal prey species for slender sole at Stations 6 and 7 but not at Station 2. The shrimp *Spirontocaris bispinosa* and unidentified fish were found in over 5% of the fish only at Station 6. Copepods were common only at Station 7.

Euphausia pacifica was a principal prey for Pacific sanddab at Stations 6 and 7. *Pandalus jordani* occurred in 26% of the fish at Station 6, but was uncommon at Station 7. Decapod crab larvae and copepods, on the other hand, were common prey only at Station 7.

Variations With Seasons or Size of Fish

Changes in the relative proportions of the major taxa of food consumed by different sizes of the four species of flatfishes are shown for "summer" (May-September) and "winter" (October-April) in Figures 2-5. Because food habits as well as sizes of fishes vary among stations (Tables 3, 6; Pearcy 1978), geographic effects are confounded in these figures.

Annelids usually dominated the diet of all size groups of these juvenile Dover sole during both seasons (Figure 2). Crustaceans appeared to decrease in importance with increasing size of fish during the winter season, but reached peaks in the summer. Mollusks (*Solegasters* spp., *Yoldia ensifera*, and unidentified pelecypods) attained peaks in the diet of intermediate-sized (200-300 mm) Dover sole, and echinoderms (mainly ophiuroids) attained a peak at a larger size of fish.

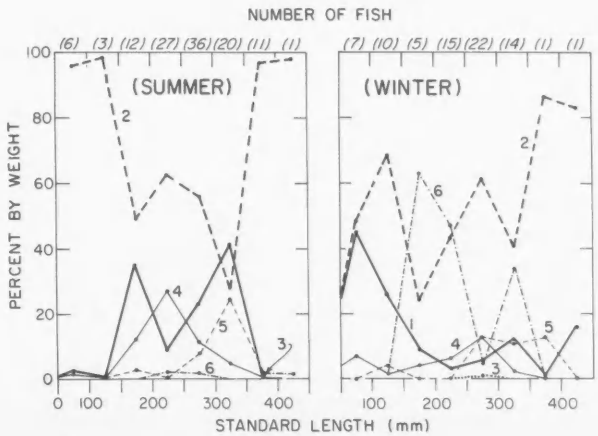

FIGURE 2.—The percent by wet weight of the major food taxa for different length groups of Dover sole for summer and winter. 1 = crustaceans, 2 = annelids, 3 = other taxa, 4 = mollusks, 5 = echinoderms, and 6 = coelenterates.

The largest difference between seasons was for coelenterates. Anemones and the feeding polyps of sea pens were unimportant constituents of the food during the summer (<2% of diet by weight) but were sometimes a major food >30% by weight) during the winter. Anemones and sea pens are probably available as prey during both seasons but for some reason only consumed in significant quantities during the winter.

Seasonal differences in the intensity of feeding were also indicated by the higher frequency of empty stomachs in winter than in summer (Table 7). The number of principal prey occurring in the diet of Dover sole was consistently larger during summer than winter regardless of fish size. Although the smaller number of stomachs with contents during the winter reduces sample size, and hence the number of taxa found, the frequency of occurrence of many of the individual taxa of polychaetes, crustaceans, and mollusks (taxa listed in Table 5) was higher in summer than winter. Bertrand (1971) found no evidence for seasonal variations in the numbers or biomass of infauna sampled with grabs at these stations. Therefore a more diverse assemblage of prey was probably available to Dover sole during the summer or fish were usually less selective during the summer than during the winter. The summer is the season of most active growth of Dover sole (Demory 1972) when intraspecific and possibly interspecific competition for food may be most intense. Decreased prey selectivity is known to occur under conditions of low food abundance or availability (Ivlev 1961; Schoener 1971).

The number of principal prey taxa generally increased with size of Dover sole (Table 7). This trend may be related to sample size (number of stomachs with food) and to the ability of large fish to consume a larger range of prey sizes than small fish. The less diverse diet of small fish resulted from ingestion of only a few species of polychaetes.

TABLE 7.—Frequency of empty stomachs (no. empty stomachs/no. fish) and the number of principal taxa (occurring in 5% or more of at least 10 observations) of prey for different sizes of Dover sole collected during summer and winter seasons.

Standard length (mm)	Frequency of empty stomachs		Number of taxa	
	Summer	Winter	Summer	Winter
51-100	6/12	15/22	9	4
101-150	—	19/29	—	8
151-200	4/16	10/15	24	12
210-250	7/34	19/34	25	18
251-300	11/47	20/42	37	17
301-350	4/24	7/21	21	15
351-400	5/16	—	41	—

Those prey types eaten by a broad size range (50-400 mm SL) of Dover sole include: *Myrochele heeri*, *Typosyllis hyalina*, *Lumbrineris* sp., Glyceridae, gammarid amphipods, pelecypods, *Megacrenella columbiana*, ophiuroids, unidentified polychaetes, and unidentified crustaceans.

Annelids and crustaceans were the major food items for rex sole (Figure 3). (Most of the rex sole represented here are juveniles.) Annelids increased in importance with an increase in the sizes of rex sole, up to 150-250 mm. This increase was associated with a decrease in the proportion by weight of crustaceans, the dominant food item for small rex sole during both seasons. Euphausiids, decapod crab larvae, copepods, and ostracods were only found as principal prey of rex sole of <200 mm. Mollusks formed only a minor portion of the diet. Differences in the FO of principal prey were not pronounced. Some polychaetes (*Sternaspis fossor*, *Myriochele heerie*, *Nothria geophiliformis*, and *Choelia pinnata*) were found more frequently in large (220-300 mm SL) rex sole.

Some seasonal differences in the diet of rex sole were evident. Euphausiids were principal prey only during the summer. Cumaceans and *Oikopleura* were more common during the winter. Principal prey that were commonly ingested by all or most size groups during both seasons were: *Sternaspis fossor*, *Goniada brunnea*, unidentified polychaetes, gammarid amphipods, and uniden-

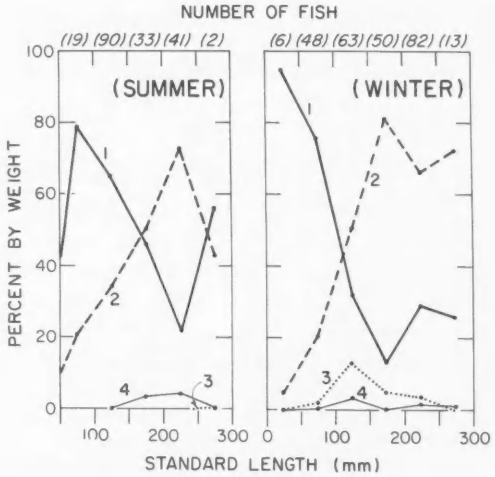

FIGURE 3.—The percent by wet weight of the major food taxa for different length groups of rex sole for summer and winter. 1 = crustaceans, 2 = annelids, 3 = other taxa, and 4 = mollusks.

tified crustaceans. Kravitz et al. (1977) listed *Nothria* spp. as frequently occurring polychaetes and *Ampelisca macrocephala*, *Hippomedon wecomus*, *Paraphoxus epistomus*(?), and *P. obtusidens* as frequently occurring amphipod prey for rex sole.

Crustaceans composed the bulk of the diet of all sizes of slender sole during both seasons (Figure 4). Annelids and "other taxa" were most important in the diet of intermediate-sized (101-200 mm) slender sole during either summer or winter. Pelagic crustaceans such as copepods, euphausiids, and crab larvae occurred frequently in the diet of small (<150 mm) slender sole, whereas polychaetes, the shrimps *P. jordani* and *S. bispinosa*, and fishes were important for large slender sole (>150 mm). Again, a larger number of principal prey taxa occurred during the summer than winter.

Crustaceans also were the most important taxa in the diet of the Pacific sanddab, except for five 201-250 mm individuals during the summer, when fishes composed 95% of the food by weight (Figure 5). Kravitz et al. (1977) found that all *C. sordidus* (90-377 mm total length) collected in May off Oregon had been feeding intensively on northern anchovy. Barss (see footnote 4) reported

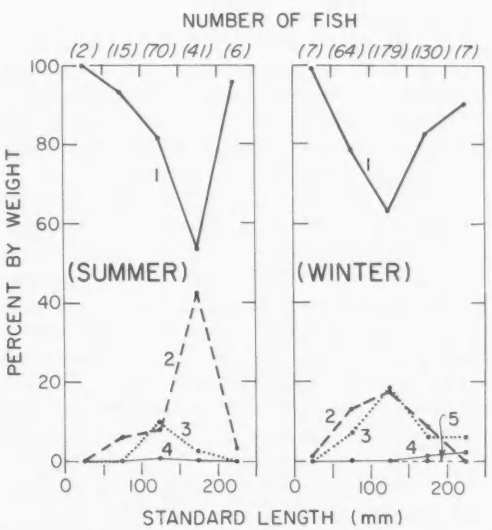

FIGURE 4.—The percent by wet weight of the major food taxa for different length groups of slender sole for summer and winter. 1 = crustaceans, 2 = annelids, 3 = other taxa, 4 = mollusks, and 5 = echinoderms.

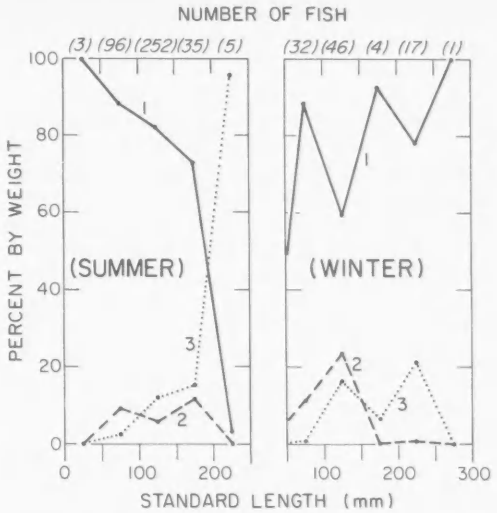

FIGURE 5.—The percent by wet weight of the major food taxa for different length groups of Pacific sanddab for summer and winter. 1 = crustaceans, 2 = annelids, and 3 = other taxa.

that sanddab eat small fishes, squids, and octopuses.

Crustaceans were the predominant prey during both seasons and for most sizes of sanddab. Euphausiids, copepods, and cumaceans occurred more frequently in small than large individuals. *Pandalus jordani*, crangonids, and fishes were most common in the diet of large Pacific sanddab.

DISCUSSION

The four common flatfishes caught in this study compose two generalized feeding types. Dover and rex soles feed almost exclusively on benthic invertebrates, mainly polychaetes and amphipods, while slender sole and Pacific sanddab prey mainly on pelagic crustaceans. The food habits of these two types are related to mouth structure and digestive morphology. Flatfishes that feed on benthos usually have asymmetrical jaws, small stomachs, and long intestines, whereas pelagic feeders have longer, symmetrical jaws with sharp teeth and long serrated gill rakers, adaptations for grasping and retaining animals that swim in midwater (Hatanaka et al. 1954; Groot 1971). Dover and rex soles belong to the benthos-feeding type and sanddab and slender sole to the pelagic-feeding type. Kravitz et al. (1977) also recognized these two feeding types among five flatfishes off

Oregon, and included rex sole as a benthophagus species and Pacific sanddab as a piscivorous-pelagic feeder.

Rae (1956, 1969) studied the feeding habits of the lemon sole, *Microstomus kitt*, and the witch, *Glyptocephalus cynoglossus*, off Scotland. Some of his results are remarkably similar to ours for the congeneric Dover sole, *M. pacificus*, and rex sole, *G. zachirus*. Both the witch and lemon sole, like the Dover and rex soles, feed predominantly on polychaetes. Crustaceans were next in importance followed by other phyla such as mollusks, echinoderms, and coelenterates. Ophiuroids and anthozoans were also eaten by both lemon sole and the witch. These similarities in diets indicate common feeding specializations within pleuronectid genera.

Although the major food of the lemon sole and witch were very similar, these two species, like the Dover and rex soles, preyed on different families or different genera of the same family so that food overlap, and presumably competition, are rare (Rae 1956, 1969). As pointed out by Rae, these differences in feeding habits reflect behaviorial differences of the fishes as well as differences in the composition of the benthic communities of which these fishes are a part. The habitats of the lemon sole and witch often differ, the lemon sole preferring hard, rocky bottoms, and the witch soft, muddy bottoms.

Both the lemon sole and witch fed most heavily during the summer. Regional differences were also marked. Polychaetes decreased in importance as prey for the witch in shallow water (<100 m), as they did in our study for Dover sole (Table 3). Rae (1939, 1956) also believed that differences in the types and quantities of food available between one area and another resulted in different growth rates of lemon sole. Sedentary polychaetes were most common as prey in areas of rapid growth.

One of the objectives of this study was to learn if differences in the availability of prey for flatfishes occurred and how it may be related to sediment types and water depth at our stations. The composition of prey of Dover sole clearly varies among stations. Polychaetes were the main food at the three deepest stations; echinoderms, coelenterates, and polychaetes were similar on a weight basis at the two 102-m stations; polychaetes, followed by mollusks, were most important at the 100-m station; and mollusks and crustaceans were most abundant at the 74-m station (Table 3). Based on the percentage by weight of major food taxa, higher similarities occurred among stations at similar depths rather than with similar sediment types: Stations 15 and 23 at 102 m and the deep stations 6, 2, and 8 at at 148-195 m (Table 4). Sediment texture at Stations 15 and 23 were dissimilar. (See Figure 1 for summary of depth and sediments for the stations.) Although Station 2 had an average sediment texture that differed from Stations 6 and 8, a thin layer of silt overlaid coarse sand at Station 2, hence the surface sediment of Stations 6, 2, and 8 were probably more similar than indicated in Figure 1.

The occurrence of individual species of polychaetes consumed by Dover sole is probably a more sensitive indicator of station differences than the biomass of major taxa. Stations 7, 15, and 23, at 100-102 m, but with different sediment types, were most similar in polychaete prey. Stations 2, 6, and 8 in deep water, at 148-195 m were again similar. Thus, these similarities in prey for these two groups of stations seem to be correlated with depth. However, polychaete prey at Station 2 (190 m) was similar to that of Station 7 (100 m), which had similar sediment type, as well as that at Stations 15 and 23 (102 m) with different sediments. Stations 22 and 15 with similar sediment types, but at different depths, had low similarity of polychaete prey.

Based on 82 species of mollusks, cumaceans, and ophiuroids sampled in 0.1-m^2 Smith-McIntyre grabs, Bertrand (1971) calculated the similarity of the fauna among the same seven stations included in this study. He also found that Stations 2, 6, and 8 formed a deep-water group of high similarity. Stations 7 and 23 (at 100-102 m) were similar, as were Stations 7 and 8, with different depths and sediment types. Gunther (1972) also calculated similarities among these same stations based on living benthic foraminifera and found that strong faunal affinities crossed depth and sediment boundaries. Again, Stations 2, 6, and 8 formed one group. Stations 2 and 7, and 15 and 22, station pairs based on sediments, were not very similar.

Similarities among the fishes caught were also strong among Stations 2, 6, and 8. The remaining stations (7, 15, 22, and 23) formed another group of high affiinity (Pearcy 1978). These two species associations agree with those described by Day and Pearcy (1968) for the continental shelf off central Oregon. They found a shallow (42-73 m) water association on a sand bottom dominated by Pacific sanddab and English sole, *Parophrys vetulus*, and an association at 119-159 m on a silty-

sand bottom dominated by slender sole and rex sole.

Shallow-water and deep-water associations are therefore evident at these stations, based on previous studies of benthic invertebrates and vertebrates, as well as the composition of the diet of Dover sole in this study. Because surface sediments were fairly similar at our three deep stations, sediment vs. depth effects could not be separated here. The lack of precise similarities of sediment types for station pairs also weakens this part of our study. Nevertheless, stations with the most similar sediment types often had low similarity of benthic fauna. We conclude that depth-related factors may have greater influence than sediment type on the composition of benthic fishes, fish food, and invertebrate fauna within the boundaries of our study area. This conclusion must be tempered, however, by the realization that other sediment parameters besides texture and percent organic matter may be important, and we simply did not study the proper sediment characteristics. We agree with Peterson (1918): "It is clear then that the character of the bottom is of fundamental importance for the presence or absence of epifauna. Nevertheless, the succession of the various types of epifauna and of the communities belonging to the level bottom cannot be explained by the character of the bottom alone."

Bertrand (1971) estimated the "edible" biomass of infauna (>1.0 mm) for demersal fishes (i.e., all infauna less holothurians, echinoids, echiurids, and burrowing anemones) at these stations from 0.1-m^2 Smith-McIntyre grab samples taken on the same cruises. He detected no seasonal variations in the wet or ash-free dry weight of this biomass fraction. The ash-free dry weights per square meter for polychaetes, mollusks, and crustaceans given by Bertrand for the seven stations are shown in Table 8. Crustacean biomass was consistently low at all stations, probably because of the ineffectiveness of the grab to sample epibenthic and motile amphipods, major food items of Dover and rex soles. There was no direct or consistent relationship between the biomass per square meter of "edible" fish food and the biomass of all fish or Dover sole. Stations with similar standing stocks of infaunal food had widely different standing stocks of benthic fishes.

TABLE 8.—Ash-free dry weights in grams per square meter of macro-infaunal fish food at the seven stations (from Bertrand 1971).

Taxa	Stn 22	7	23	15	6	2	8
Polychaetes	0.04	0.17	0.30	0.08	0.17	0.14	0.19
Mollusks	4.50	1.10	1.74	2.09	0.20	0.16	0.07
Crustaceans	0.006	0.005	0.001	0.004	0.008	0.004	0.003
Total	4.55	1.28	2.04	2.17	0.38	0.30	0.26

Station 22, the beach sand station—with the lowest organic carbon in the sediment of all stations—supported a fairly low biomass of fish, but the largest biomass of edible fish food, 4.55 g/m^2, and the largest biomass of invertebrate macrobenthos. Conversely, Wigley and McIntyre (1964) found the largest biomass in finer sediments off Massachusetts, and Lie and Kisker (1970) found that the shallow-water sand communities off Washington had a lower average standing stock of infauna than deeper communities on the shelf. The large biomass at Station 22 is composed primarily of the bivalves *Acila castrensis* and secondarily of *Tellina salmonea*. Both of these mollusks were principal prey of Dover sole only at Station 22 (Table 5). Although the frequency of occurrence of these two mollusks in Dover sole stomachs was only 10%, mollusks composed 58% by weight of the food of Dover sole at this station. Thus Dover sole are versatile predators, changing their diets opportunistically in response to changes of prey availability.

The dominant fish at Station 22 was Pacific sanddab, primarily a pelagic feeder. Mollusks were not principal prey. *Acila* and other burrowing animals are unavailable as food for fishes adapted for pelagic feeding, illustrating a basic reason for the lack of any direct relationships between edible fish food and fish biomass.

The average biomass of Dover sole was directly related to the biomass of their principal food, polychaetes, at the seven stations (Figure 6). Station 22, where Dover sole consumed principally mollusks, had the lowest biomass of both polychaetes and Dover sole; intermediate values of biomass of both fish and food are found at the three deep stations (2, 6, 8). The three stations at about 100 m (2, 7, and 15) differed markedly in standing stocks of both polychaetes and Dover sole. This positive correlation ($r = 0.73$) of standing stocks of predator and prey implies that Dover sole selected habitats within our study area where their prinicpal preferred food was most abundant regardless of depth and bottom type. Of more fundamental interest is the fact that standing stocks of polychaetes may indicate the amount of food available to Dover sole, and perhaps the production rates of polychaetes at the different stations. Similar direct relationships between standing

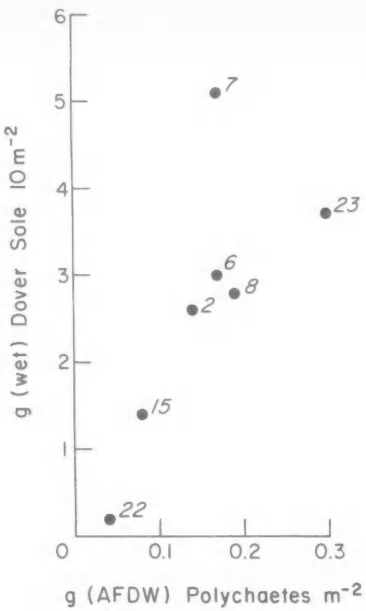

FIGURE 6.—The relationship between average standing stocks of prey (grams ash-free dry weight of polychaetes per square meter) and predator (grams wet weight of Dover sole per 10 m at the seven stations.

stocks of predator and prey have been elucidated by Brocksen et al. (1970) for the biomass of phytoplankton and zooplankton and for zooplankton and sockeye salmon among ecosystems with different productivities. This is the first example, to our knowledge, of such a relationship for the marine benthos.

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SKIPJACK TUNA, *KATSUWONUS PELAMIS*, HABITAT BASED ON TEMPERATURE AND OXYGEN REQUIREMENTS

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ABSTRACT

The habitat of skipjack tuna, *Katsuwonus pelamis*, has generally been assumed to be the warm surface layers of tropical and subtropical ocean, where most of these fish are seen and caught. But experiments with captive Hawaiian skipjack tuna imply that their habitat is more restricted, with boundaries defined by both temperature and dissolved oxygen. The lower temperature limit appears to be about 18° C. The upper temperature limit apparently varies with size of the fish, from 30° C or more for small individuals to as little as 20° C for the largest. Skipjack tuna also require water with unusually high concentrations of dissolved oxygen, at least 3.0-3.5 ml/l (4-5 ppm), for long-term survival. If our Laboratory findings with captive skipjack tuna accurately define their natural habitat, only the smallest of these animals can inhabit the warm surface waters of the tropics; those larger than 4-5 kg must inhabit the thermocline. Our hypothesis, which can be tested, explains many features of the known distribution of skipjack tuna in the eastern and central Pacific Ocean.

For skipjack tuna, *Katsuwonus pelamis* (Linnaeus), the question "Where are the fish?" is particularly hard to answer. Their habitat is known only in the most general terms. These fish are found in tropical and subtropical waters of all oceans, at surface temperatures between 15° and 30° C. Because they are caught most frequently by methods such as trolling, purse seining, and pole-and-line fishing, it is generally assumed that skipjack tuna inhabit the surface mixed layer. Japanese longline gear, which fishes well below the sea surface, catches very few skipjack tuna, and then only on the hooks which fish nearest the surface (Yabe et al. 1963). In a review of the literature on this species, Matsumoto and Skillman[3] pointed out that the sea-surface temperature range where most skipjack tuna are caught varies from one fishery to another. Off Tasmania and southeast Australia, the range is 15° to 18° C. Off Japan and South America, the range appears to be 20° to 24° C, while the fishery off southern India operates in water of 28° to 29° C. The Hawaii fleet fishes skipjack tuna all year, in water with surface temperatures ranging from 23° to 27° C, with the majority of catches in the warm, summer months.

Because studies of the occurrence of wild skipjack tuna in relation to sea-surface temperature yield such disparate results from one area to another, and because the total temperature range, 15° to 30° C, includes more than half of the surface area of the world's oceans, we have worked with captive animals in a series of experiments intended to define more precisely their physiological requirements. Results of three of these studies (Neill et al. 1976; Dizon et al. 1977; Gooding and Neill[4]) provided information on the skipjack tuna's temperature and dissolved oxygen requirements which, taken together, appear to define the actual habitat of this species in nature.

We present here a summary of the physiological studies and their results, which suggest specific temperature and dissolved oxygen values that define the spatial limits of the skipjack tuna habitat. With the resultant temperature and dissolved oxygen values, we have mapped the habitat of the skipjack tuna using averaged oceanographic data from the eastern Pacific Ocean.

These habitat maps present our hypothesis in a testable form. If skipjack tuna in nature have the same requirements as those studied in captivity, their distribution should, on average, correspond

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[3]Matsumoto, W. M., and R. A. Skillman. Synopsis of biological data on skipjack tuna, *Katsuwonus pelamis* (Linnaeus). Manuscr. in prep. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, P.O. Box 3830, Honolulu, HI 96812.

[4]Gooding, R. M., and W. H. Neill. Respiration rates and low oxygen tolerance limits in skipjack tuna, *Katsuwonus pelamis*. Manuscr. in prep. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, P.O. Box 3830, Honolulu, HI 96812.

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with the habitat volume shown on the maps. If, under normal oceanographic conditions, they occur in significant numbers well outside of the mapped habitat volume the hypothesis is invalid, and we should look for evidence of adaptations (behavioral, physiological, and genetic) which were not evident in our work with captive fish. If the distribution of skipjack tuna is more restricted than our habitat maps would indicate, we should look for factors in addition to temperature and dissolved oxygen (e.g., turbidity) which might further limit the habitat. Salinity is not apt to be one of these factors, however, since captive skipjack tuna do not respond to rather drastic changes in this variable (Dizon 1977).

More immediate and definitive tests of the hypothesis can be made by tagging wild skipjack tuna of various sizes with tags capable of sensing and telemetering depth, temperature, and dissolved oxygen.

TEMPERATURE AND OXYGEN REQUIREMENTS

Lower Temperature Limit

Dizon et al. (1977) determined that 15° C was the lower lethal temperature limit for skipjack tuna. They subjected recently caught, apparently healthy individual fish to water temperatures which decreased 1° or 5° C/day, starting at ambient temperature (about 24° C), with other skipjack tuna held continuously at ambient temperature as controls. All seven of the test animals survived and fed until temperature had declined to 18° C; at 17° C all but one fish stopped eating, and one fish died. None of the fish survived 15° C for more than a few hours. Accordingly, we have selected 18° C as the lowest water temperature which Hawaii skipjack tuna can withstand for prolonged periods of time without significant increases in mortality.

This preliminary estimate of the lower temperature limit is essentially identical with the value obtained by Williams (1970) from a comparison of fishery catch data with sea-surface temperatures in the eastern Pacific. Williams found that most skipjack tuna were caught in water with temperatures between 29° and 20° C, with diminishing catches down to temperatures between 18° and 17° C, and no catches in colder waters.

Three large (ca. 70 cm) Hawaiian skipjack tuna released with tags that telemetered swimming depth were found to spend >85% of their time in water warmer than 20° C and <10% in water colder than 18° C (Dizon et al. in press).

In the western South Pacific, skipjack tuna have been caught in water near 15° C, off Tasmania (Robins 1952) and off eastern Australia (G. I. Murphy, Division of Fisheries and Oceanography, CSIRO, New South Wales, Australia, 1977, pers. commun.). These fish probably belong to a different subpopulation (Fujino 1972) than fish found in Hawaii.

Lower Dissolved Oxygen Limit

Gooding and Neill (see footnote 4) examined the effects of low dissolved oxygen concentrations on skipjack tuna. Their animals, habituated in open tanks with circulating, essentially saturated seawater (4.5 ml O_2/l, or 6.4 ppm), were transferred to tanks in which the concentration of dissolved oxygen could be maintained at a preselected constant subsaturation level. Temperatures in both sets of tanks were ambient, 23° to 24° C. Dissolved oxygen concentrations down to 1.0 ml/l (1.4 ppm) were used. Resistance times and swimming speeds were measured, and general behavior was observed for up to 4 h in each experiment. Under their experimental conditions, Gooding and Neill concluded that hypoxic stress was first manifest, through changes in swimming behavior and speed, at about 2.8 ml/l (4.0 ppm), a value fairly typical for fish. Lethal oxygen levels, leading to death in 4 h or less, were found to be higher than those for any other freshwater or marine fish thus far studied. Only one fish (out of six) survived 4 h at 2.5 ml/l (3.5 ppm), and none survived as long as 2 h at still lower concentrations. At higher oxygen values, above 2.5 ml/l, all skipjack tuna tested in this study survived at least 4 h.

Because we sought to estimate the lowest dissolved oxygen concentrations that skipjack tuna can tolerate indefinitely without significant stress, we have chosen a conservative value of 3.5 ml/l (5 ppm) as the lower limit to the skipjack tuna's habitat, where temperature and other variables are not limiting.

Upper Temperature Limit

The case for an upper temperature limit to the skipjack tuna's habitat is somewhat less direct. Three small (30-35 cm) individual skipjack tuna maintained in water warmed 1°C/day survived

until the temperature reached 33°C, when two died; the other lived until the water reached 34°C (Dizon et al. 1977). Skipjack tuna have a high metabolic rate and a countercurrent heat exchanger in their circulatory system which dramatically restricts heat loss through the gills. This accounts for the fact that freshly caught wild skipjack tuna can have red muscle core temperatures as high as 11°C above that of the surrounding water (Stevens and Fry 1971).

Temperature excesses of this magnitude could lead to dangerously high muscle temperatures if they occur in the warmer parts of the ocean. To examine this possibility we use a heat balance model developed for skipjack tuna by Neill et al. (1976) which yields an estimate of temperature excess in the red muscle core as a function of size and metabolic activity (Figure 1a). Actual muscle core temperatures are found by adding the values shown in this figure to the temperature of the surrounding water, for any given size fish. Clearly, large skipjack tuna in surface waters of the tropics must either tolerate high muscle core temperatures, or reduce their metabolic activity substantially below the 3 mg O_2 g^{-1} h^{-1} level.

But skipjack tuna appear to avoid heating their muscle tissue much above 35°C (Stevens and Fry 1971). This upper limit must place a similar upper limit on the water temperatures which skipjack tuna can inhabit, unless they can thermoregulate physiologically or behaviorally. In Figure 1b, 35°C is taken as the upper limit for the red muscle core, and temperature excesses of Figure 1a are subtracted from that value to arrive at an estimate of the upper temperature limits for the habitat of skipjack tuna, as a function of size. If the values thus obtained are valid, these fish should be able to live anywhere in the ocean when they are small, but they should be limited to lower and lower environmental temperatures as they grow. The largest known skipjack tuna, weighing approximately 16 kg, would—if active enough—be confined to water temperature near 18°C, which is also their approximate lower limit.

SKIPJACK TUNA HABITAT HYPOTHESIS

We hypothesize that skipjack tuna of the central and eastern Pacific Ocean occupy a primary habitat—a volume of water whose properties they can tolerate indefinitely—which is 18°C or warmer, but cooler than the upper limits for normally active animals shown in Figure 1b, provided that the dissolved oxygen concentration is at least 3.4 ml/l (5 ppm). Skipjack tuna can presumably

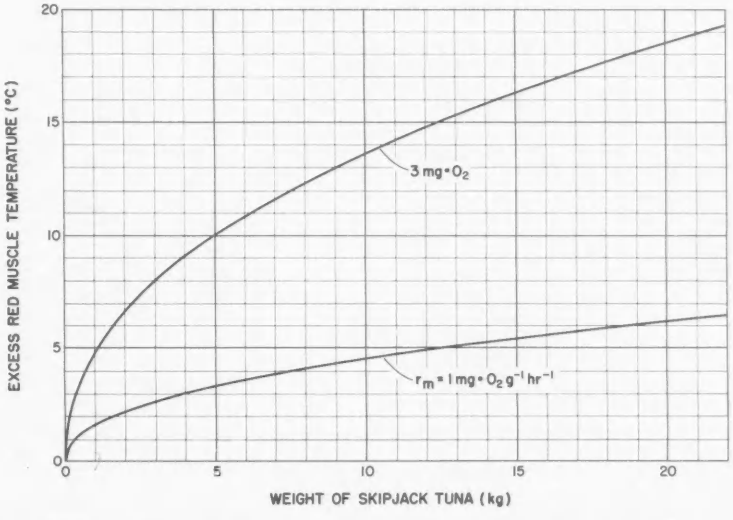

FIGURE 1a.—Calculated excess of internal temperature, over that of the surrounding water, in red muscle for skipjack tuna of all known sizes. Values are shown for a measured minimum (anesthetized) level of metabolic activity (lower line) and our estimate of the mean metabolic activity for normally active animals (upper line), triple the minimum level. (From Neill et al. 1976.)

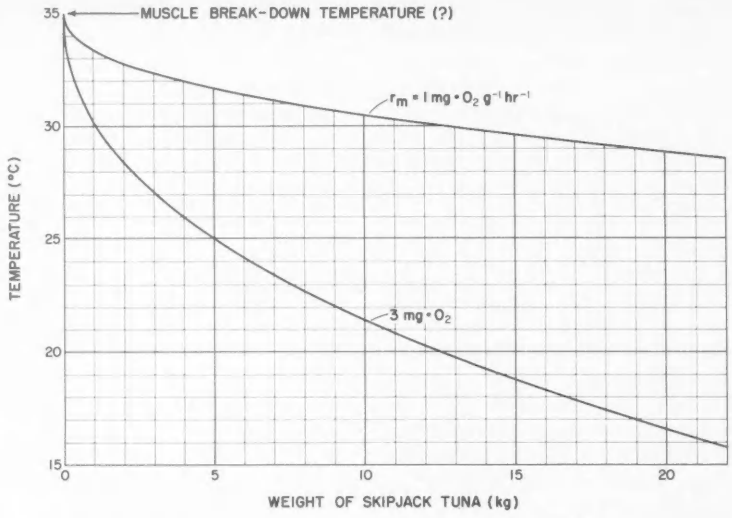

FIGURE 1b.—Maximum tolerable water temperature for skipjack tuna as a function of size for the same two rates of metabolic activity illustrated in Figure 1a. Based on calculated internal temperature excesses and the assumption that damage to red muscle tissue occurs above 35°C.

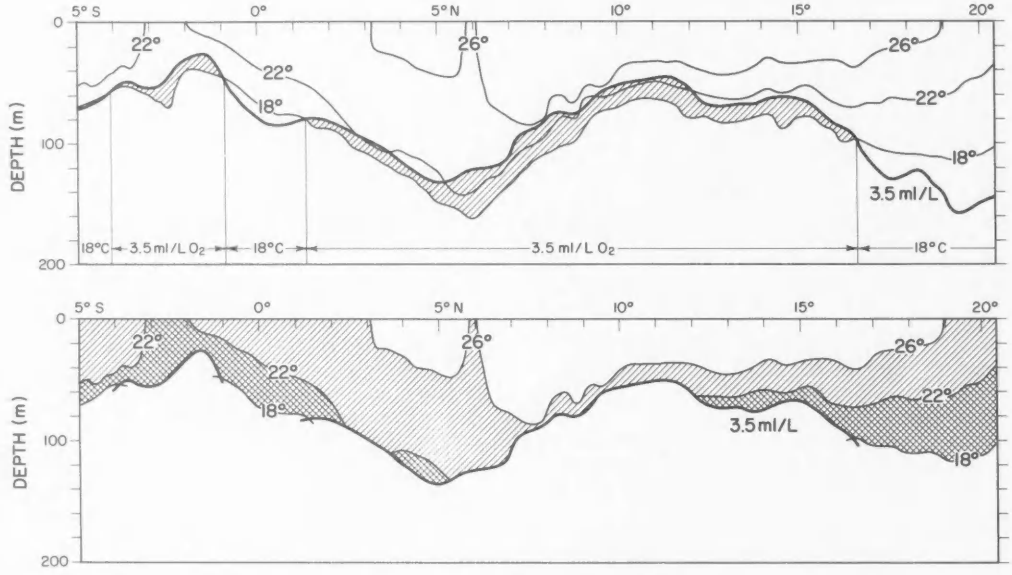

FIGURE 2.—Upper panel: Temperature and dissolved oxygen (selected isopleths only) along long. 119° W, eastern Pacific Ocean, August 1967 (Love 1972). Lower limits of the skipjack tuna habitat are assumed to be either 18°C or 3.5 ml/l dissolved oxygen, as indicated. The hatched layer should be warm enough for these fish, but oxygen deficient. Lower panel: Hypothesized habitat layers for skipjack tuna of two sizes, 4 kg (entire hatched area) and 9 kg (cross hatched area only) in the same section. Fish <4 kg could presumably live anywhere between the sea surface and the lower limits, 18°C or 3.5 ml/l of dissolved oxygen.

leave their primary habitat only for limited periods of time without suffering thermal or oxygen stress. Prolonged excursions to colder water would require increased activity and thus more dissolved oxygen and food. Skipjack tuna could stay in the warm upper layers only if they would reduce their physical activity, or tolerate overheating. Hypothetical consequences of these conditions are illustrated in Figure 2 which shows the hypothetical layers along long. 119° W for skipjack tuna of two sizes. The 4-kg fish are those most abundant in catches by the eastern Pacific fishery; 9-kg fish are the largest normally found there, and then only in certain areas such as the Revillagigedo Islands (ca. lat. 17° N, long. 112° W).

The deeper limit of the habitat should be the same for skipjack tuna of all sizes. The upper limit is deeper and more restrictive for larger fish, which find essentially no habitable water between lat. 5° and 12° N, a distance of more than 700 km or 400 n.mi. Larger fish also have much less continuous access to the sea surface than those weighing 4 kg. Only skipjack tuna of the smallest size commonly found in this area (< 4 kg) could inhabit all of the water above the lower limits in Figure 2.

Figures 3 to 6 are maps of a hypothetical skipjack tuna habitat for the entire central and eastern Pacific Ocean, based on oceanographic station data used in preparing the Oceanographic Atlas of the Pacific Ocean (Barkley 1968). For these maps,

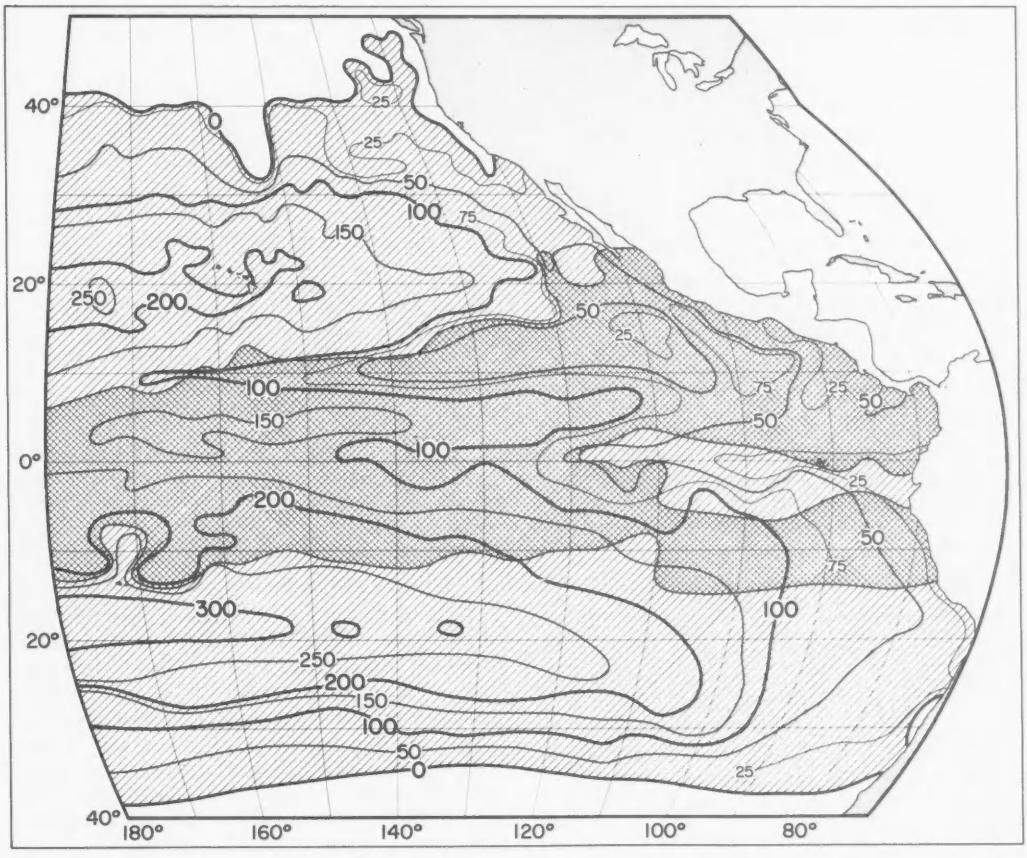

FIGURE 3.—Hypothetical maximum depth (meters) of the skipjack tuna habitat in the eastern Pacific Ocean, as determined by the depth of the 18°C isotherm (hatched area) or the 3.5 ml/l (5 ppm) isopleth of dissolved oxygen (cross hatched area). Contour interval is 50 m except for a few areas near the coast, where a 25-m contour interval is used.

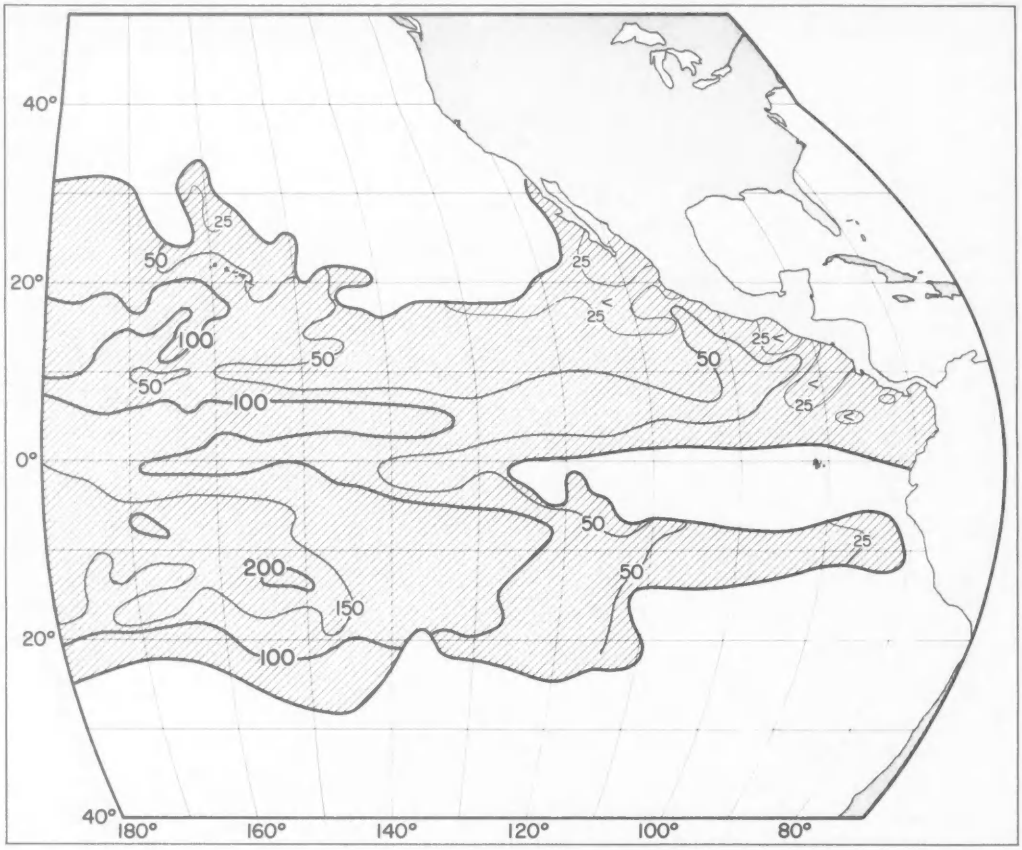

FIGURE 4.—Hypothetical minimum depth of the skipjack tuna habitat in the Pacific Ocean east of long. 180°, for fish weighing about 6.5 kg (14 lb) which are limited to water cooler than 24°C. Contours show the depth, in meters, of the 24°C isotherm.

station data were averaged within 2° areas of latitude and longitude, for all months, to approximate annual mean conditions.

Figure 3 shows the hypothetical "floor" of the skipjack tuna habitat, i.e., maximum depths (in meters) for this species. In Figure 3, the unhatched areas off the Pacific coast of the Americas, and at latitudes higher than about 40° in both hemispheres, indicate water which, at all depths, is colder on average than 18°C; presumably skipjack tuna would not normally be present.

Figure 4 shows the minimum habitat depth or ceiling for 6.5-kg fish. Outside of the hatched area annual mean surface temperatures are <24°C, and 6.5-kg fish would normally have access to all of the water column above the habitat floor (Figure 3), up to and including the sea surface.

Figure 5 shows the hypothesized habitat layer thickness for 6.5-kg skipjack tuna. In some areas, there is no water cooler than 24°C with more than 3.5 ml/l dissolved oxygen, so in these areas there is no habitat for 6.5-kg or larger fish; such areas are double hatched on Figure 5. Extensive regions around these areas have habitat layer thickness of 10 m or less, and large areas of the equatorial Pacific Ocean have <25 m of habitat layer thickness. This rather thin layer can lie beneath as much as 150 m of water warmer than 24°C (at lat. 4°N, long. 170°W, e.g.). North of the Hawaiian Islands, the opposite situation is present: a 150-m thick habitat layer lies under 25 to 50 m of water

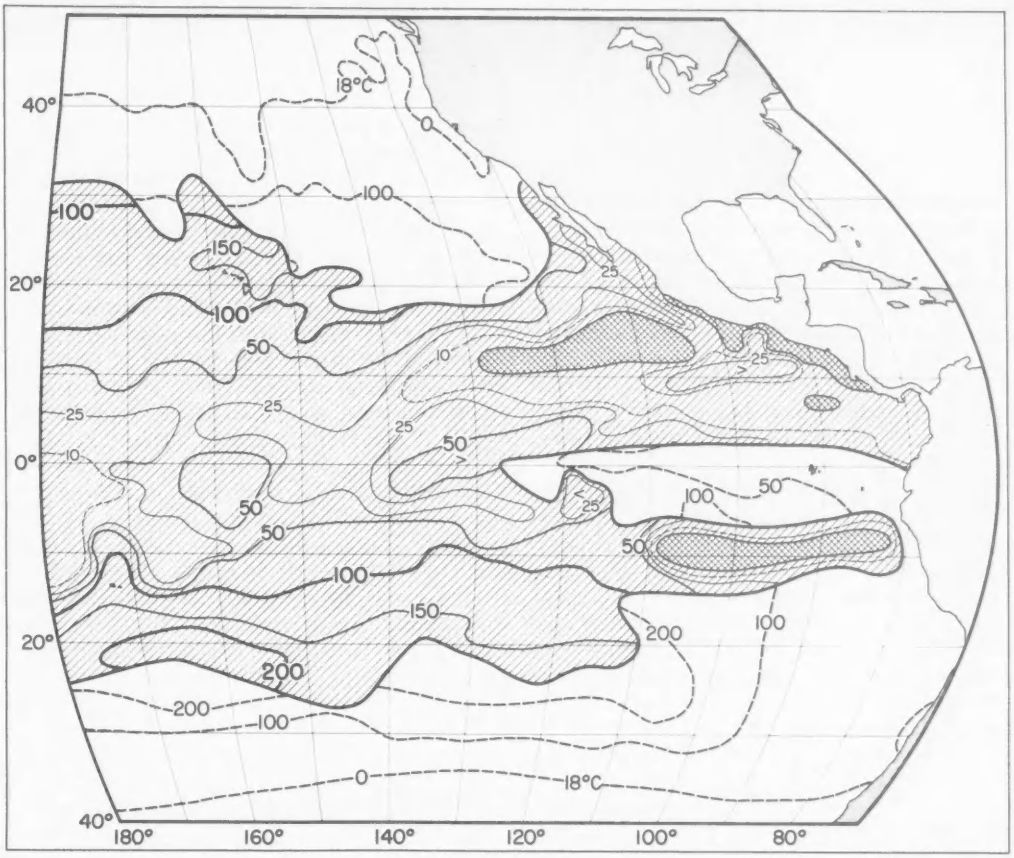

FIGURE 5.—Thickness of the hypothetical habitat layer (meters), for 6.5-kg skipjack tuna in the eastern and central Pacific Ocean. Contours were obtained by subtracting depths of the upper habitat limit (Figure 4) from the lower one (Figure 3). In the crosshatched areas off Mexico and Peru, there should be no habitat suitable for fish of this or larger sizes. In the hatched area, water warmer than 24°C is present above the habitat layer. Immediately beyond this area the habitat (dashed depth contours) extends to the sea surface. Outside of the 18°C surface isotherm, the water is probably too cold for skipjack tuna.

warmer than 24°C. Clearly, the South Pacific Ocean offers the roomiest habitat to large skipjack tuna, and in fact some of the largest known individuals of this species were caught slightly south of Tahiti (lat. 17°S, long. 150°W), according to catch records of longline fishing boats (R. A. Skillman, Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812, 1977, pers. commun.).

An interesting feature of the habitat map for 6.5-kg fish (Figure 5) is a channel of relatively cool and adequately oxygenated water some 200 km off the coast of Mexico. This channel should allow skipjack tuna as large as 6.5 kg to pass from the Baja California fishery to the equatorial fishery, or vice versa, when fish as small as 4 kg would find stressful conditions for hundreds of kilometers on either side of that channel. Seasonal and year-to-year closure or shifting of this channel could readily explain puzzling variations in the distribution of skipjack tuna catches in the eastern Pacific.

Figure 6 shows areas of presumably stressful environment (zero habitat thickness) in the eastern tropical Pacific for fish of various sizes and therefore temperature limitations. Skipjack tuna >11 kg should find no habitat at all within the shaded area. Fish 4 kg in size would find no habitat within the smallest contour (temperatures above

26° C). Fish weighing <4 kg should find some thickness of habitable water, within and just below the upper mixed layer, everywhere in the eastern tropical Pacific.

DISCUSSION

Although we anticipate that temperature and dissolved oxygen will prove to be primary determinants of the habitat of skipjack tuna in all oceans, it is possible that limiting values of these variables may differ from one population or region to another. The lowest temperature (ca. 15° C) at which skipjack tuna are caught in Australian waters (Robins 1952) is considerably lower than in the eastern Pacific. The fish caught off Australia may also differ in their ability to tolerate warm or low-oxygen water.

The gross features of the distribution of skipjack tuna in the eastern tropical Pacific, where only small skipjack tuna are found in large numbers (Williams 1970), agree with the hypothesis. Those areas where large skipjack tuna do occur (Matsumoto 1975) are outside of the hatched area in Figure 6; the Revillagigedo Islands, e.g., are just north of the hatched area, and Tahiti is well south of it.

The hypothetical habitat proposed here explains why skipjack tuna leave the northern fishery of the eastern Pacific when they reach a certain size. To find cooler, better oxygenated water as they grow, these fish must move out of the eastern tropical Pacific toward higher latitudes in the central Pacific. Also, they must then spend less time at or near the sea surface, since the thermocline, where they live, is generally much deeper in the central Pacific, and the water above the thermocline is too warm to permit normal activity. This size-specific movement in response to the environment is consonant with Rothschild's (1965) migration model for the eastern Pacific skipjack tuna population. It also suggests a mechanism for the evolution of migratory processes, an important topic in marine ecology.

For several reasons, existing fishery data are inadequate for making a refined judgment of our skipjack tuna-habitat hypothesis: 1) Commercial fishery data generally include neither information

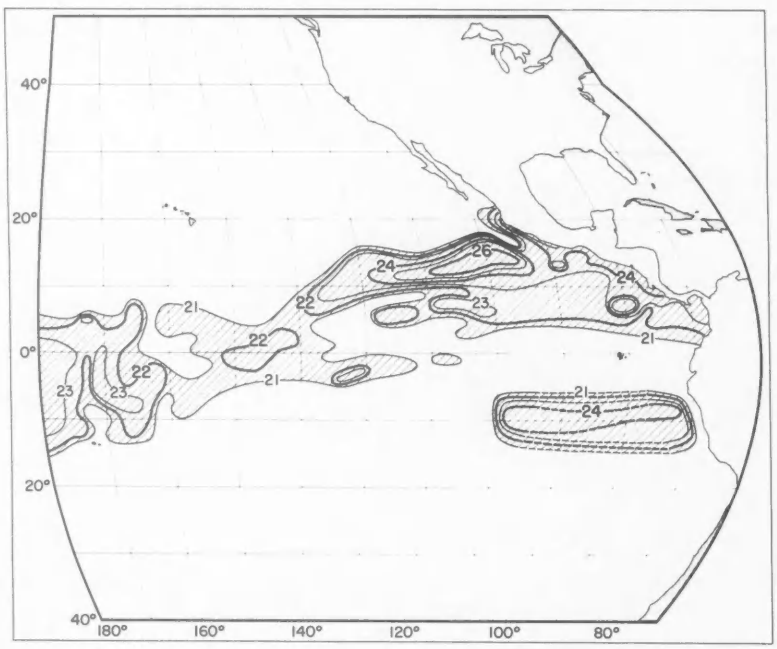

FIGURE 6.—Average water temperature in the eastern Pacific Ocean at those depths where the concentration of dissolved oxygen is 3.5 ml/l. Deeper water is cooler and lower in oxygen, shallower water is warmer and has more oxygen. See Figure 1b for the relationship between skipjack tuna size and upper temperature limits.

on individual sizes of skipjack tuna composing the catch nor synoptic information on the vertical distribution of temperature and dissolved oxygen in the fishing area. 2) The degree to which catch per unit effort measures fish abundance may vary greatly with gear type, fish size, and environmental conditions. For example, the habitat hypothesis implies that purse seines (which fish the upper 50 m or so of the water column) should be most effective in those parts of skipjack tuna habitat with a shallow floor. In fact, the eastern Pacific purse seine fishery operates almost entirely in waters with a skipjack tuna habitat-floor at depths of 50 m or less (c.f. our Figure 3 and fig. 1 of Matsumoto 1975). Efforts to catch skipjack tuna by purse seining in Hawaiian waters—where the habitat-floor lies at depths near 200 m (Figure 3)—have been ineffectual (Murphy and Niska 1953). Green (1967) reported strong positive correlations between the success of purse seining for eastern Pacific skipjack tuna and yellowfin tuna, *Thunnus albacares*, and the presence of shallow ($\leq$60 m to top), steep ($\geq$0.55°C cm^{-1}) thermoclines. 3) Commercial fishermen naturally fish only where they expect to find and catch fish; thus, fishing effort tends to be very unevenly distributed.

A partial test of the habitat hypothesis might be achieved through experimental fishing in and near the hatched areas of Figure 6; fishing effort, the sizes of captured skipjack tuna, and vertical distributions of temperature and dissolved oxygen would need to be measured at each fishing location. But, experimental fishing—even if conducted in a thorough and systematic fashion—might not yield a conclusive test of the hypothesis, because there would still be no guarantee that catch per unit effort accurately reflected fish abundance (reason 2 above).

We advocate, instead, the application of ultrasonic telemetry to test the skipjack tuna-habitat hypothesis. Because skipjack tuna tagged with ultrasonic transmitters tend to stay with their school (Yuen 1966) and because skipjack tuna schools tend to be homogeneous with respect to fish size (Brock 1954), the track of a single tagged fish could be taken as representative of a large number of normally behaving, similarly sized fish. Pressure-sensitive ultrasonic transmitters (like that described by Luke et al. 1973) would permit continuous monitoring of fish position in all three spatial dimensions through time. Spatial-temporal coordinates of fish could then be compared with synoptic data on vertical distributions of temperature and dissolved oxygen. A few dozens of such comparisons, for fish of various sizes in waters with diverse vertical distributions of temperature and dissolved oxygen, would constitute a valid and sufficient test of the habitat hypothesis. Toward this end, preliminary telemetry work is now underway at this Laboratory.

SUMMARY

Work with captive skipjack tuna at this Laboratory has yielded information on the temperature and dissolved oxygen requirements of this species. If these laboratory results apply to skipjack tuna in nature, they provide new insight into the evolution of migration in skipjack tuna populations, make it possible to account for the geographic distribution of skipjack tuna on the basis of environmental conditions, and provide means for predicting their movements in major fisheries such as those of the eastern tropical Pacific.

In particular, we suggest that only young skipjack tuna can inhabit tropical surface waters, and that the habitat of adult skipjack tuna in the tropics is the thermocline and not the warmer surface layer, as has generally been thought. Since the thermocline in many areas is too oxygen-poor to support these active fish and the well-oxygenated surface layer is too warm for adult skipjack tuna, only heat-tolerant young skipjack tuna can live in those areas. As they grow, these fish are forced to move into areas where well-oxygenated water of the proper temperature is more readily available.

Up to now, it has not been possible to trace the movements of migrating skipjack tuna largely because they move through areas of many millions of square miles, at unknown depths. Knowledge of their temperature and dissolved oxygen requirements dramatically reduces the scope of the problem: the fish should be in a well-defined layer of water, of directly and easily measured thickness, whose geographic extent can be sharply defined with either historical or current oceanographic observations.

ACKNOWLEDGMENTS

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HISTORICAL TRENDS AND STATISTICS OF THE SOUTHERN OSCILLATION, EL NINO, AND INDONESIAN DROUGHTS

WILLIAM H. QUINN, DAVID O. ZOPF, KENT S. SHORT, AND RICHARD T. W. KUO YANG[1]

ABSTRACT

A 116-yr Southern Oscillation index record was used in conjunction with environmental data and reports from various authors on disturbances to the anchoveta fishery, marine bird life, etc. off the Peruvian coast, to infer the occurrence of past El Niño type events and their intensities. The resulting long time history substantiates our earlier report that certain Southern Oscillation index features are excellent precursors of subsequent El Niño type events. We suggest that statistics derived from this time history could be useful in the management of the Peruvian anchoveta fishery and for providing long-range outlooks on El Niño type activity.

Anomalously heavy precipitation in the central and western equatorial Pacific and Indonesian droughts were closely associated with El Niño type events.

In recent years the world demand for fishmeal has continued to increase, as has the world population. The Peruvian anchoveta fishery, which ordinarily provides over half the world's supply of fishmeal, has become a critical resource; and anything that affects the output of this fishery is of world-wide significance. Johnson and Seckel (1977) reported that the catch in this fishery declined from a high of over 12 million tons (about 1/5 of the total world catch of all fish) in 1970 to about 2 million tons in 1973. Although overfishing in 1970-71 may have contributed heavily to this decrease in anchovy catch, the strong El Niño of 1972-73 was undoubtedly also a major cause for the precipitous decline in catch (Figure 1). However, the 1975 catch was still only about 25% of the record 1970 catch, the 1976 catch remained low, and the target for 1977 has now been reduced to 2 million tons of anchoveta and other fish such as sardines and hake. Apparently the unfavorable environmental conditions caused by the very weak event of early 1975 and the moderate El Niño of 1976-77 have not only contributed to the delay in recuperation of the fishery, but also are causing a further degradation of it. In early October 1977 the Fisheries Ministry of Peru said (according to a Reuters wire service report) that the stocks were believed to be so low that the anchoveta fishing, which was suspended in May 1977, would not resume until the second half of 1978.

Statistical information pertaining to the historical occurrence of El Niño type events is presented to: 1) aid in long-term fishery assessment (Peruvian anchoveta fishery); 2) provide a basis for speculative long-range outlooks on event occurrence (beyond a year in advance); and 3) guide long-range predictions (1-12 mo in advance). Relationships between El Niño type events, Southern Oscillation index trends, index component trends, and Indonesian droughts are shown and discussed.

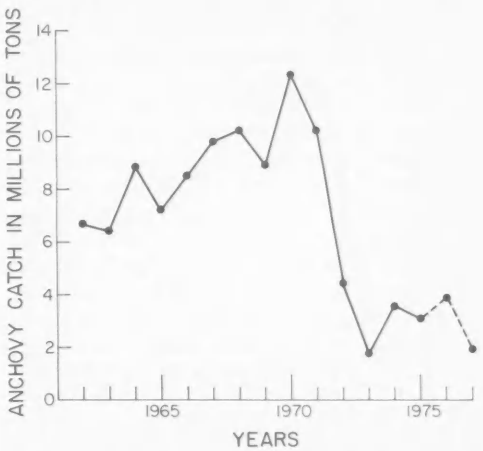

FIGURE 1.—The Peruvian anchovy catch for the period 1962-76 as obtained from the Industrial Fishery Products Market Review and Outlook for June 1977 (National Marine Fisheries Service 1977). The 1976 figure is a preliminary value. The 1977 figure is the Peruvian Fishery Ministry target value for anchovies and other species such as sardine and hake, as reported by Reuters wire service on 19 October 1977.

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Wooster (1960), Idyll (1973), Miller and Laurs (1975), and Caviedes (1975) furnished background information on El Niño; Quinn (1974) discussed monitoring and prediction; and Berlage (1957, 1966), Troup (1965), and Quinn (1971, 1976) provided background information on the Southern Oscillation and how it relates to phenomena discussed in this paper.

Definitions for terms frequently used in this paper follow: The Southern Oscillation was originally identified by Walker (1924). It was loosely defined by Berlage (1966) as a fluctuation in the intensity of the intertropical general atmospheric and hydrospheric circulation over the Indo-Pacific region. The fluctuation is dominated by an exchange of air between the South Pacific subtropical high and the Indonesian equatorial low. The differences in sea level atmospheric pressure between sites representing the South Pacific subtropical high and sites representing the Indonesian equatorial low are used as indices to represent the Southern Oscillation (Quinn 1974).

The El Niño type event refers to the appearance of anomalously warm sea surface temperatures and abnormally heavy rainfall in the equatorial Pacific and an invasion of anomalously warm surface water off the coast of Peru and southern Equador. This event, which is brought about by relaxation from a prolonged period of strong southeast trades, is represented by falling and low Southern Oscillation indices (Quinn 1974). The magnitude of the interannual relaxation and its timing with relation to the regular seasonal relaxation (Southern Hemisphere summer) appear to determine the strength of the El Niño invasion along the Peruvian coast. Heavy central and western equatorial Pacific precipitation usually starts a few or more months after El Niño initially sets in, but this may not always be the case. By using the term "El Niño type" we avoid arguments over what is and what is not an El Niño and can then account for events that evolve in a similar manner but vary in timing, intensity, and extent.

The anti-El Niño refers to the contrasting situation when a strengthening and strong southeast trade system prevails (represented by rapidly rising and high Southern Oscillation indices). At such times we can expect strong upwelling (due to the divergent equatorial flow under the influence of strong southeast trades and equatorial easterlies), anomalously low sea surface temperatures, and abnormally low amounts of rainfall over the equatorial Pacific. Also, off the coast of Peru, we find strong coastal upwelling, low sea surface temperatures, lower than average sea level, and generally favorable physical environmental conditions for biological productivity (due to the upwelling of nutrient-rich water from lower levels).

METHODS

Data Processing

Atmospheric pressure and much of the rainfall data before 1961 were obtained from the World Weather Records (Clayton 1927, 1934; Clayton and Clayton 1947; U.S. Department of Commerce 1959, 1968). Data for 1961-76 were obtained from Monthly Climatic Data for the World (U.S. Department of Commerce 1961-76). We were primarily interested in the large-scale interannual changes. Therefore, we eliminated regular oscillations from the data, such as the diurnal cycle, by using monthly mean values (or monthly amounts, for rainfall), and the seasonal or annual cycle by subtracting long-term average or normal monthly values from the actual monthly values. Data so processed show no particular regularity and no apparent cycle (Panofsky and Brier 1965). The filtered and unfiltered monthly anomalies were used to detect, identify, and evaluate any unusual changes that took place.

Our interests were focused on fluctuations of an intermediate scale (Southern Oscillation), with periods ranging between about 1 and 6 yr. The remaining short period fluctuations in the anomalies were eliminated by filtering with a low pass filter. At the other end of the time scale, there may be a gradual change of the variate over many years which is part of oscillations that are long compared with the record. These extremely long, gradual changes were not a factor in our study.

In earlier papers (e.g., Quinn 1974, 1976) the 12-mo running mean was applied directly to monthly values of pressure, pressure differences (indices), rainfall, etc. as a low pass filter. This filter not only smoothed the data to some extent but also eliminated the annual cycle. To more clearly define the interannual fluctuations (Southern Oscillation), we recently switched to the use of the triple 6-mo running mean filter on the monthly anomalies, which requires three successive passes of the 6-mo running mean over the data. It results in smoother plots and more clearly defined peaks and troughs, which are of particular assistance in establishing long-term trends. The

loss of 3 mo time with each application of the 6-mo running mean is a drawback to its use in forecasting, so we also use the 3-mo running mean and monthly plots of anomalies for locating inflection points and evaluating trends on a more immediate basis in support of forecasts.

Anomaly trends for several indices were maintained in time section plots (Figure 2a, b) to evaluate the Southern Oscillation and its expected effects on the southeast trade system. Although these limited records (25-30 yr) clearly showed the close association of low indices with El Niño type activity, and high indices with anti-El Niño conditions (Quinn 1974, 1976), it was essential to extend the study over a much longer period to determine how frequently these climatic extremes occurred

The World Weather Records were searched for the longest and most complete atmospheric pressure records which could be used to extend our study into the past. Madras, India (1841-1976); Bombay, India (1847-1976); Djakarta, Indonesia (1866-1974); and Darwin, Australia (1882-1976) were within the area noted by Berlage (1957, 1966) to reflect Southern Oscillation-related pressure changes in the Indonesian equatorial low pressure cell. Santiago, Chile (1861-1976) had the only long pressure record that could possibly represent Southern Oscillation-related pressure changes affecting the South Pacific subtropical high pressure cell. Although Santiago is generally to the east of the subtropical high, it does reflect these pressure changes (Berlage 1957, 1966).

Correlations were run between the Tahiti-Darwin index and the Santiago-Darwin index on data for 1935-76 to further substantiate use of the Santiago-Darwin index for representing the Southern Oscillation and related El Niño type activity. The Tahiti-Darwin index was used for this comparison since it and the Santiago-Darwin index showed similar amplitudes in their interannual fluctuations. The similarity was due to the fact that Tahiti and Santiago are separated by analogous distances from the usual core of activity in the subtropical high (see fig. 10 in Berlage 1957, or fig. 10 in Bjerknes 1969). At zero lag the correlation coefficient between the two indices was 0.88. The maximum correlation was 0.89 when the Tahiti-Darwin index led the Santiago-Darwin index by 1 mo.

Figure 3a-h shows the triple 6-mo running mean plots of pressure anomalies for Madras (1841-1976), Bombay (1847-1976), Djakarta (1866-1974), and Darwin (1882-1976). They also show similar plots of pressure index anomalies for Santiago-Bombay (1861-81) and Santiago-Darwin (1882-1976). The anomaly plots were used along with other data in the evaluation of El Niño type events reported over the past 135 yr.

Classification of Events

The classification of El Niño type events by intensity is highly subjective since no two cases are exactly alike with regard to time of onset, duration, areal extent, thermal departure, degree of devastation, etc. Determinations concerning event occurrence and intensity were primarily based on: 1) reported disruptions of the anchoveta fishery and marine bird life off the coast of Peru; 2) scientific reports which discussed events that affected the coastal regions of Peru and southern Ecuador [e.g., Eguiguren (1894), Frijlinck (1925), Murphy (1926), Hutchinson (1950), Sears (1954), Schweigger (1961)]; 3) hydrological data for the Peruvian coastal region; 4) sea-surface temperature data along the coasts of Peru and southern Ecuador; 5) rainfall at coastal stations in Peru and southern Ecuador; 6) height of preevent peaks and depth of relaxation troughs in Southern Oscillation index trends; 7) related indications from index component trends (when pressure components from only one core of the Southern Oscillation were available); 8) sea-surface temperatures over the equatorial Pacific; 9) rainfall data for islands in the central and western equatorial Pacific.

We categorized events as strong, moderate, weak, or very weak, depending on the intensity of the activity and the time of year that it occurred. The true El Niño sets in during the first half of the year. A symptom which is common to El Niños is the presence of anomalously high sea-surface temperatures off the coasts of southern Ecuador and Peru. Other frequently mentioned features include a southward coastal current, heavy rainfall, red tide (aguage), invasion by tropical nekton, and mass mortality of various marine organisms including guano birds, sometimes with subsequent decomposition and release of hydrogen sulfide (known as El Pintor) (Wooster 1960).

Strong El Niños are recognized as such by all investigators; they involve positive sea-surface temperature anomalies along the coast in excess of 3°C, they display most of the aforementioned features, and the anchoveta fishery is seriously

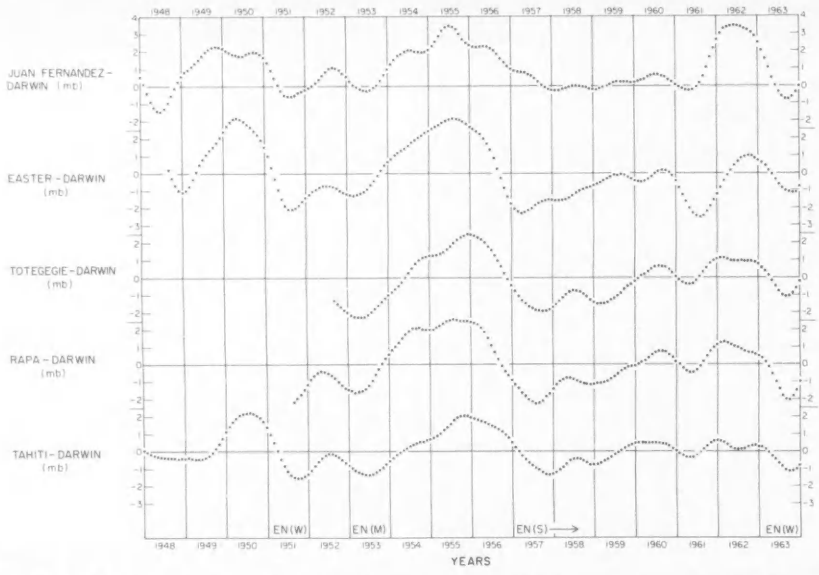

FIGURE 2a.—Triple 6-mo running mean plots of anomalies of the difference in sea level atmospheric pressure (millibars) between Juan Fernandez Is. (33°37′S, 78°50′W) and Darwin, Australia (12°26′S, 130°52′E), between Easter Is. (27°10′S, 109°26′W) and Darwin, between Totegegie (23°06′S, 134°52′W) (Gambier Is.) and Darwin, between Rapa (27°37′S, 144°20′W) (Austral Is.) and Darwin, and between Tahiti (17°33′S, 149°20′W) (Society Is.) and Darwin for 1948-63. El Niño type events (EN) are indicated in strong (S), moderate (M), and weak or very weak (W) intensity.

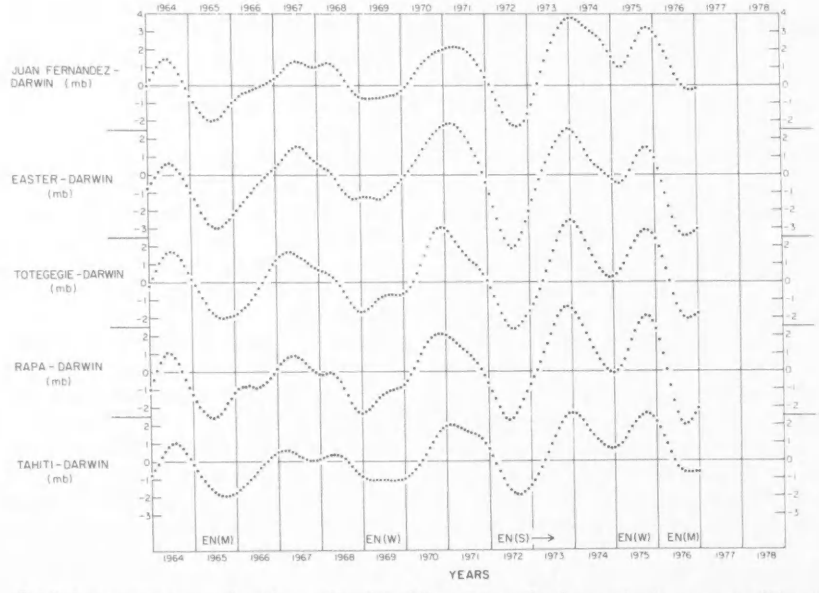

FIGURE 2b.—Triple 6-mo running mean plots of anomalies of the difference in sea level atmospheric pressure (millibars) between Juan Fernandez Is. and Darwin, between Easter Is. and Darwin, between Totegegie and Darwin, between Rapa and Darwin, and between Tahiti and Darwin for 1964-76. El Niño type events (EN) are indicated in strong (S), moderate (M), and weak or very weak (W) intensity.

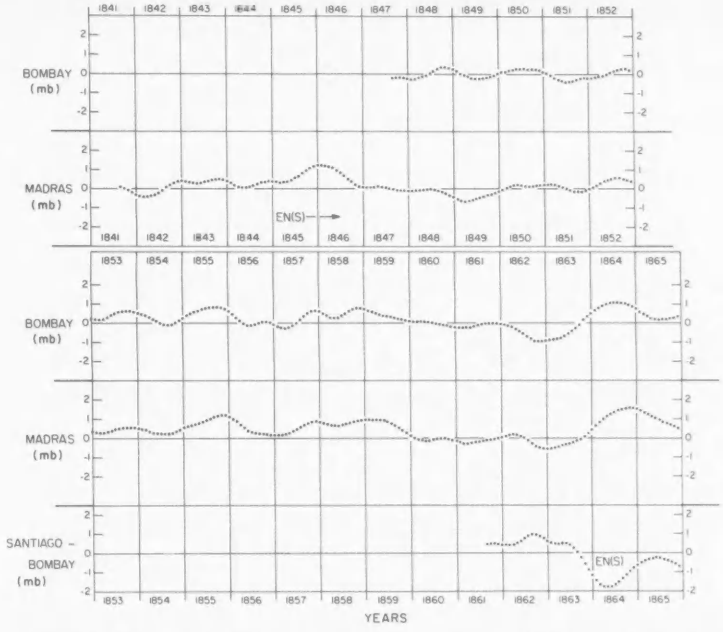

FIGURE 3a.—Triple 6-mo running mean plots of sea level atmospheric pressure anomalies (millibars) for Bombay (18°54′N, 72°49′E), India (1847-65) and for Madras (13°00′N, 80°11′E), India (1841-65); also triple 6-mo running mean plot of difference in atmospheric pressure anomalies between Santiago (33°27′S, 70°42′W), Chile and Bombay (1861-65). El Niño type events (EN) are indicated in strong (S) or moderate (M) intensity.

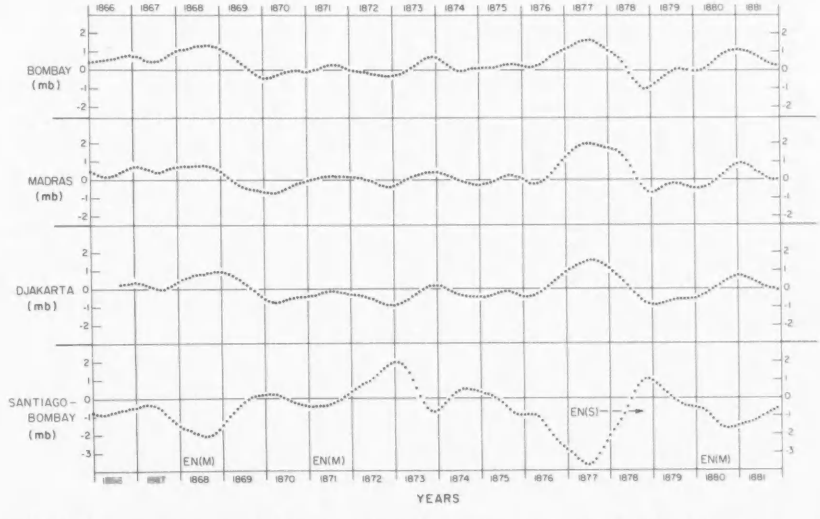

FIGURE 3b.—Triple 6-mo running mean plots of sea level atmospheric pressure anomalies (millibars) for Bombay and Madras, India, and Djakarta (06°11′S, 106°51′E), Indonesia (1866-81); also, triple 6-mo running mean plot of difference in atmospheric pressure anomalies between Santiago and Bombay (1866-81). El Niño type events (EN) are indicated in strong (S) or moderate (M) intensity.

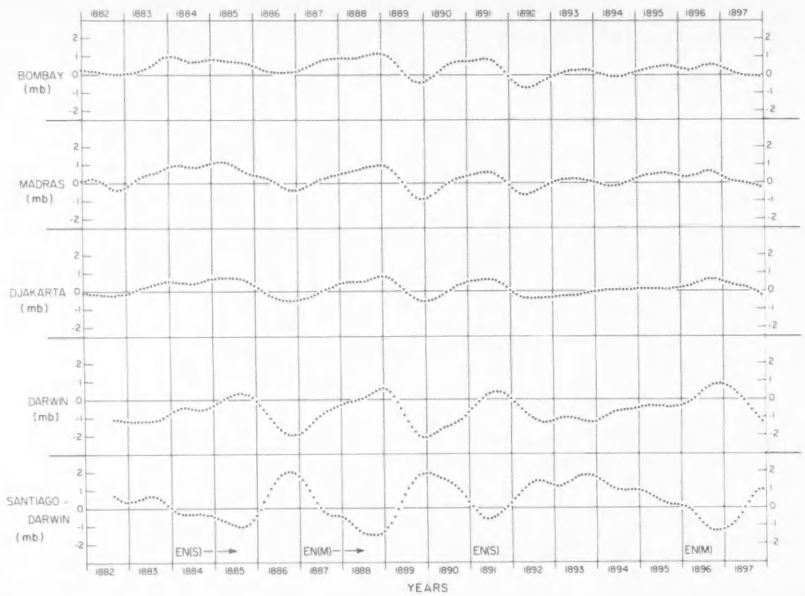

FIGURE 3c.—Triple 6-mo running mean plots of sea level atmospheric pressure anomalies (millibars) for Bombay, Madras, Djakarta, and Darwin (12°26′S, 130°52′E), Australia (1882-97); also triple 6-mo running mean plot of difference in atmospheric pressure anomalies between Santiago and Darwin (1882-97). El Niño type events (EN) are indicated in strong (S) or moderate (M) intensity.

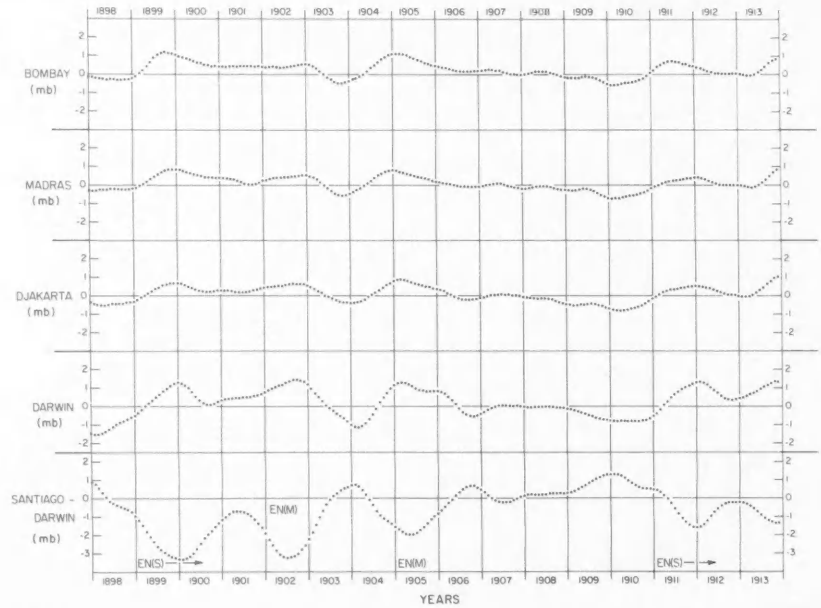

FIGURE 3d.—Triple 6-mo running mean plots of sea level atmospheric pressure anomalies (millibars) for Bombay, Madras, Djakarta, and Darwin (1898-1913); also, triple 6-mo running mean plot of difference in atmospheric pressure anomalies between Santiago and Darwin (1898-1913). El Niño type events (EN) are indicated in strong (S) or moderate (M) intensity.

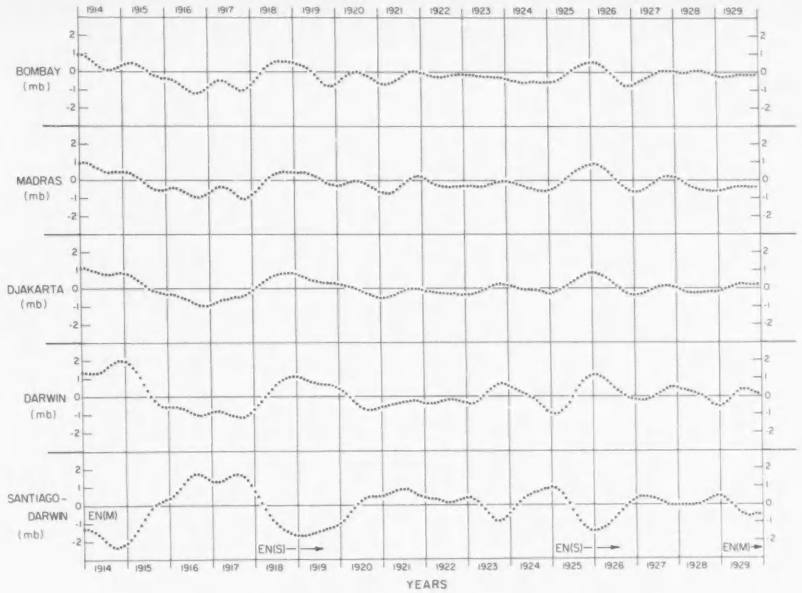

FIGURE 3e.—Triple 6-mo running mean plots of sea level atmospheric pressure anomalies (millibars) for Bombay, Madras, Djakarta, and Darwin (1914-29); also, triple 6-mo running mean plot of difference in atmospheric pressure anomalies between Santiago and Darwin (1914-29). El Niño type events (EN) are indicated in strong (S) or moderate (M) intensity.

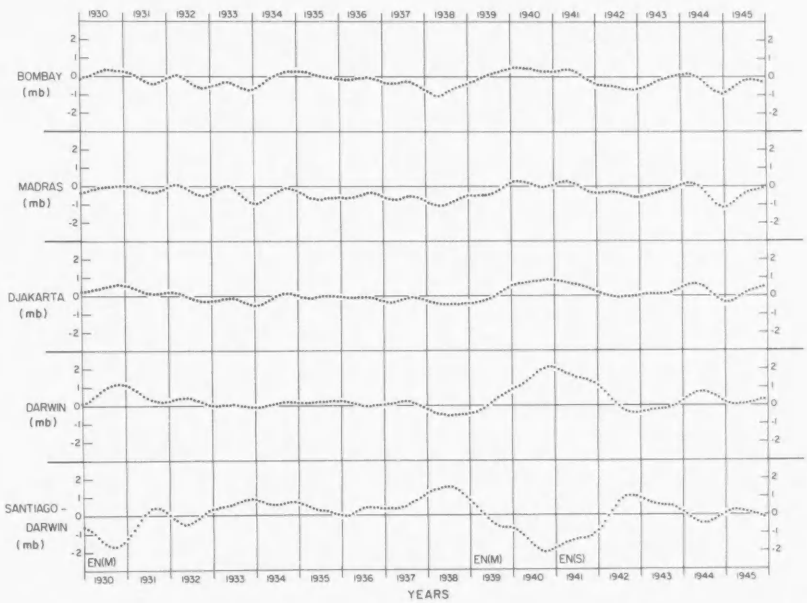

FIGURE 3f.—Triple 6-mo running mean plots of sea level atmospheric pressure anomalies (millibars) for Bombay, Madras, Djakarta, and Darwin (1930-45); also, triple 6-mo running mean plot of difference in atmospheric pressure anomalies between Santiago and Darwin (1930-45). El Niño type events (EN) are indicated in strong (S) or moderate (M) intensity.

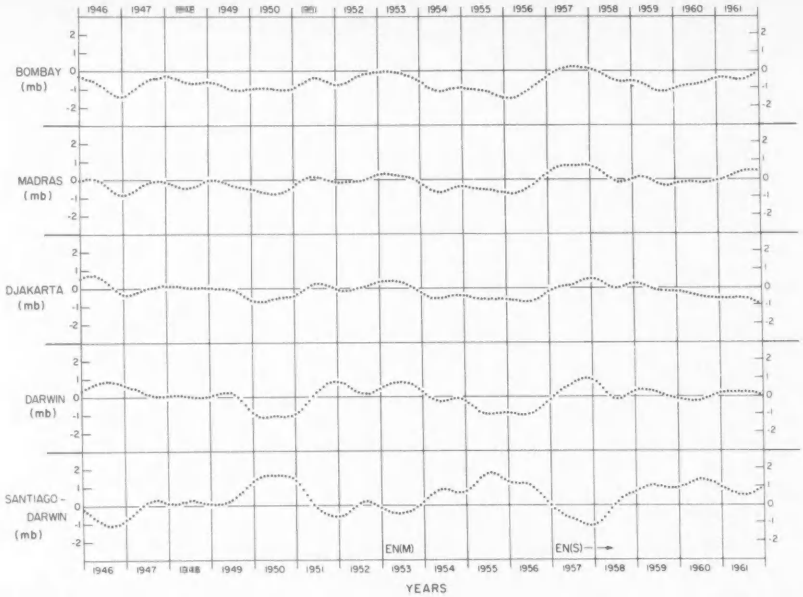

FIGURE 3g.—Triple 6-mo running mean plots of sea level atmospheric pressure anomalies (millibars) for Bombay, Madras, Djakarta, and Darwin (1946-61); also, triple 6-mo running mean plot of difference in atmospheric pressure anomalies between Santiago and Darwin (1946-61). El Niño type events (EN) are indicated in strong (S) or moderate (M) intensity.

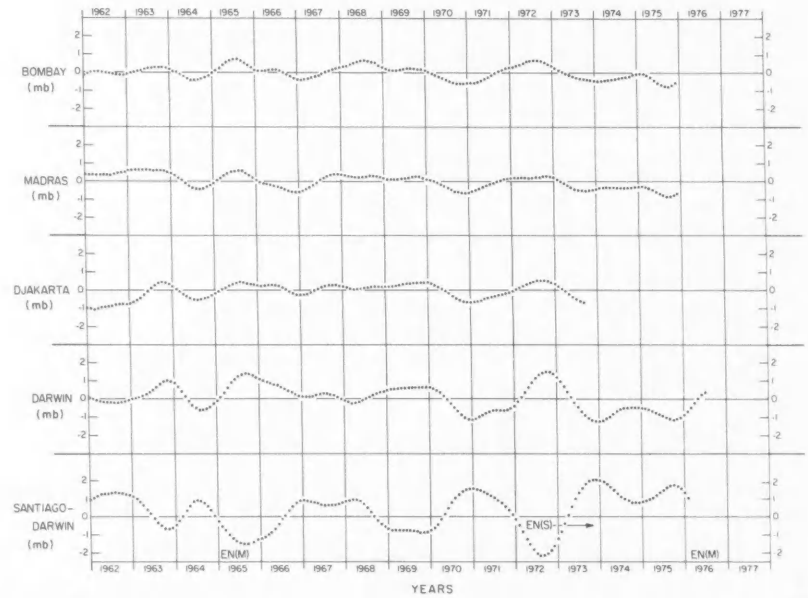

FIGURE 3h.—Triple 6-mo running mean plots of sea level atmospheric pressure anomalies (millibars) for Bombay, Madras, Djakarta, and Darwin (1962-76); also, triple 6-mo running mean plot of difference in atmospheric pressure anomalies between Santiago and Darwin (1962-76). El Niño type events (EN) are indicated in strong (S) or moderate (M) intensity.

affected (e.g., the 1957-58 and 1972-73 cases of recent years). Moderate cases are recognized as El Niños by most investigators, and display typical El Niño features to a lesser degree; maximum monthly sea-surface temperature anomalies along the coast usually peak in the 2.0°-3.5°C temperature range (e.g., the 1953, 1965-66, and 1976-77 cases of recent years). The effects of a moderate El Niño on the anchoveta fishery are considerable, but less serious than for the strong category.

Weak events may or may not be recognized as El Niños by investigators; maximum monthly sea-surface temperature anomalies along the coast usually peak in the 1.0°-2.5°C temperature range, but may appear relatively late in the year (e.g., the 1951 and 1969 cases of recent years). Very weak events are not considered to be El Niños; maximum sea-surface temperature anomalies, if they penetrate into the coast, are in the 0°-2°C range (e.g., the 1963 and 1975 events). The weak and very weak categories are included in this discussion because the difference between weaker and stronger events depends not only on the height of the preevent index anomaly peak and the subsequent degree of relaxation reflected in the southeast trade strength, but also on the timing of this interannual relaxation. If the timing is in phase with the regular annual relaxation (Southern Hemisphere summer and early fall), a moderate or strong event is likely to occur; if they are out of phase, a weak or very weak event is likely. Relaxation troughs that occur near the end of the year are usually associated with high Peruvian coastal sea temperature anomalies in the latter half of the year. The weak and very weak events may not be of significance to the Peruvian anchoveta fishery, but they do show up in the western equatorial Pacific rainfall and their larger scale aspects may be significant from the standpoint of associated global fluctuations. Figure 4 shows an example of how the recent events were reflected in the Tarawa rainfall.

The weaker events were included as EN(W) in Figure 2a, b, since we have a fairly large amount of evidence available from 1950 on. They were not included in Figure 3a-h due to the decreasing availability of evidence as we reach further back in time. However, these weaker events, ascertained to the best of our ability from available data

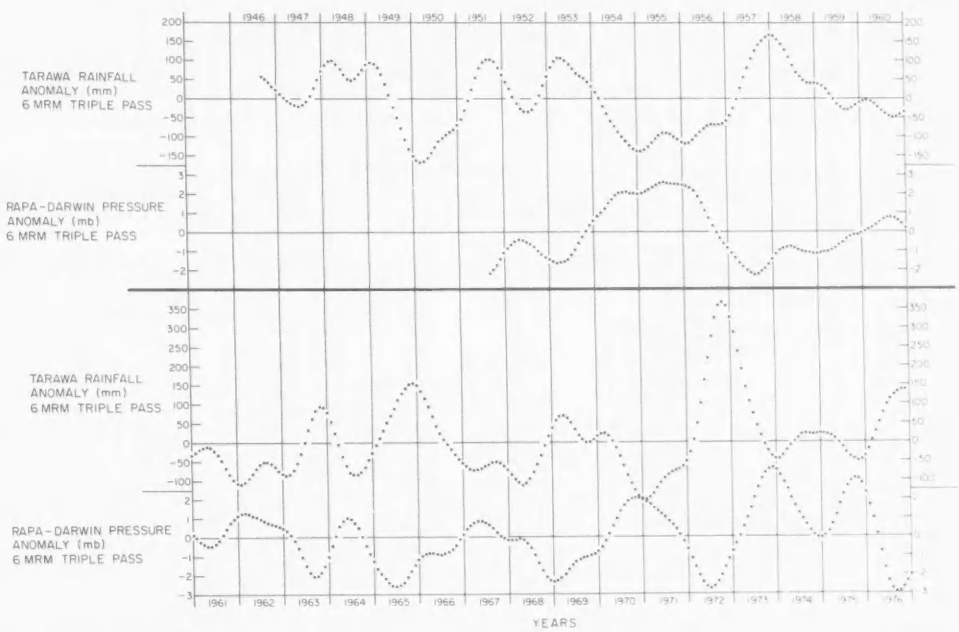
TARAWA RAINFALL ANOMALY (mm) 6 MRM TRIPLE PASS
RAPA-DARWIN PRESSURE ANOMALY (mb) 6 MRM TRIPLE PASS
TARAWA RAINFALL ANOMALY (mm) 6 MRM TRIPLE PASS
RAPA-DARWIN PRESSURE ANOMALY (mb) 6 MRM TRIPLE PASS
1946 1947 1948 1949 1950 1951 1952 1953 1954 1955 1956 1957 1958 1959 1960
1961 1962 1963 1964 1965 1966 1967 1968 1969 1970 1971 1972 1973 1974 1975 1976
YEARS

FIGURE 4.—Triple 6-mo running mean plot of anomalies of the difference in sea level atmospheric pressure (millibars) between Rapa (27°37'S, 144°20'W) (Austral Is.) and Darwin (12°26'S, 130°52'E), Australia compared with a similarly filtered plot of Tarawa (01°21'N, 172°55'E) (Gilbert Is.) rainfall anomalies (millimeters).

and literature, are included in Table 1; and, the typical index and index component trends associated with them can be noted in Figure 3a-h.

Eguiguren's (1894) data were evaluated to extend the record back even further. He classified rainfall at Piura, Peru (lat. 5°5'S, long. 80°38'W) into five categories: dry (0), light (1), moderate (2), good (3), and extra ordinary (4). Considering the distribution of events over the period 1891-1976 in relation to Eguiguren's rainfall category distribution for 1791-1890, it appeared that we could relate his category 4 to a strong El Niño, category 3 to a moderate El Niño, and categories 2 and 1 to weak and very weak events respectively. One must realize that for this Peruvian desert area long-term average rainfall values have little meaning, since averages combine data from the more-frequent drought years with data from the smaller number of event years when significant rainfall may occur. A year when an average amount of rain fell is likely to have been a year when an event occurred. Whereas the categories 3 and 4 rainfall situations were likely to have been associated with El Niño, there is no assurance that the categories 1 and 2 rainfalls were associated with the oceanic events.

A study of presumed event occurrences (based on Eguiguren's information) in relatiion to trends of the Southern Oscillation indices and index components for a period when overlapping data records were available (1841-90) showed a high degree of compatibility. Table 1 lists years in accordance with Eguiguren's rainfall classification as well as our interpretation of event intensity after considering his indications, the index and index component trends, and the various data and information sources listed early in this section.

After 1790 and prior to 1841, when no pressure records were available for a cross-check, we avoided the weak event category, but accepted Eguiguren's stronger categories 3 and 4 events. Events occurring prior to 1791, as reported by Frijlinck (1925), were considered to be of the strong variety. Sources for each event are listed in Table 1.

STATISTICAL STUDY OF EL NINO TYPE EVENTS

From a practical standpoint, we were concerned with the question of when the next event is likely to occur and what its intensity might be. Therefore, this study referred to the onset times for separate events and the interval between onset times. When the year immediately following the year of onset reflected an event of equal or lower intensity, it was assumed that the initial event extended into this next year or that the effects of the initial event held over into the early part of the next year; and, the whole situation was treated as a single event. However, when a weaker initial event preceded a stronger event in a following year they were treated as two separate events,

TABLE 1.—Year of onset of El Niño type events, 1726-1976, as classified according to event intensity by Eguiguren (1894), left, and the present authors, right (events below intensity 3 were not accepted prior to 1841 when pressure data became available). Numbers refer to event intensity: 1, very weak; 2, weak; 3, moderate; and 4, strong. Asterisks indicate onset of events considered separate (see text).

Year	Event intensity		Key to source	Year	Event intensity		Key to source	Year	Event intensity	Key to source	Year	Event intensity	Key to source
*1726		(3)	G	*1852	2	(2)	B, PC	*1896	(3)	PI, R	*1943	(2)	G, T, R
*1728		(4)	A, G	1854	2		B	*1899	(4)	D, PI, R	1944	(2)	PI, T
*1763		(4)	A	*1855		(2)	PC	1900	(3)	PI, R	*1946	(1)	PI, R
*1770		(4)	A	*1857	2	(2)	B, PC	*1902	(3)	PI, R	*1948	(1)	PI, T, R
*1791	4	(4)	A, B	1862	2		B	*1905	(3)	PI, R	*1951	(2)	G, PI, T
*1803	2		B	*1864	4	(4)	A, B, PI	*1911	(4)	F, E, PI	*1953	(3)	G, E, T
*1804	4	(4)	B	1866	2		B	1912	(3)	F, PI	*1957	(4)	G, L, PI
*1814	4	(4)	B	*1868	1	(3)	B, C, PI	*1914	(3)	G, PI, R	1958	(4)	G, L, PI
*1817	3	(3)	B	*1871	4	(3)	A, B, C	*1917	(2)	H	*1963	(1)	PI, R
*1819	3	(3)	B	*1873		(2)	PI	*1918	(4)	C, D, PI	*1965	(3)	M, PI, T
*1821	3	(3)	B	*1875	1	(1)	B, PC	1919	(3)	D, PI, R	*1969	(2)	PI, T, R
*1824	3	(3)	B	*1877	4	(4)	A, B, PI	*1923	(2)	H, PI	*1972	(4)	N, O, PI
*1828	4	(4)	A, B	1878	4	(4)	A, B, PI	*1925	(4)	D, E, PI	1973	(4)	N, O, T
1829	1		B	*1880	2	(3)	B, PI	1926	(4)	I, PI, T	*1975	(1)	P, PI, T
*1832	3	(3)	B	*1884	4	(4)	A, B, PI	*1929	(3)	G, I, PI	*1976	(3)	Q, PI, T
*1837	3	(3)	B	1885		(3)	PI	1930	(3)	G, PI, T			
*1844	3	(2)	B, PC	*1887	2	(3)	B, PI	*1932	(2)	E, I, J			
*1845	4	(4)	B, C, PC	1888	2	(3)	B, PI	*1939	(3)	E, J, T			
1846	2	(3)	B, PC	1889	1	(1)	B, PI	1940	(2)	C, PI, T			
*1850	2	(2)	B, PC	*1891		(4)	D, E, PI	*1941	(4)	E, K, T			

Key	Source
A	Frijlinck (1925)
B	Eguiguren (1894)
C	Hutchinson (1950)
D	Murphy (1923, 1926)
E	Sears (1954)
F	Forbes (1914)
G	Schweigger (1961)
H	Lavalle (1917, 1924)
I	Shepard (1930, 1933)
J	Mears (1944)
K	Lobell (1942)
L	Wooster (1960)
M	Guillén (1967)
N	Idyll (1973)
O	Caviedes (1975)
P	Wyrtki et al. (1976)
Q	Quinn (1976)
R	Rainfall (equatorial and/or Peruvian)
T	Sea-surface temperature off Peru
PC	Pressure component of Southern Oscillation index
PI	Southern Oscillation pressure index

since an additional contribution was introduced in the following year. The foregoing assumptions were based on findings from a study of the Southern Oscillation index trends and associated events over recent decades when more data were available for case history studies.

Our study of strong events was limited to the period 1763-present (Table 2, Figure 5), since the break of 35 yr between 1728 and 1763 was 14 yr longer than the longest subsequent break between events, and there was no way of eliminating the possibility that one or more strong events might have gone unreported over the 35-yr gap. These data indicate that given a strong El Niño, there is a 35% probability of having another strong event in 7-8 yr, and an 82% probability of having one within the next 15-16 yr. Considering all available data, the time between onsets of separate strong events was never <7 yr.

For strong and moderate events (Table 3, Figure 5) the record was limited to the period 1791-present when data for both categories were available. For strong, moderate, and weak events (Table 4, Figure 5) the record was limited to 1842-present, so we would have at least one index component trend available for cross-checking the less prominent weak events. (Madras pressure data became available in 1841.) With the addition of very weak events (Table 5, Figure 5), we limited our record to 1862-present in order to have an index trend available for cross-checking the more obscure very weak events. (The Santiago-Bombay index became available in 1861.)

Cases were noted where relaxation from a large preevent index anomaly peak appeared to be a two or more stage process. [This type development was

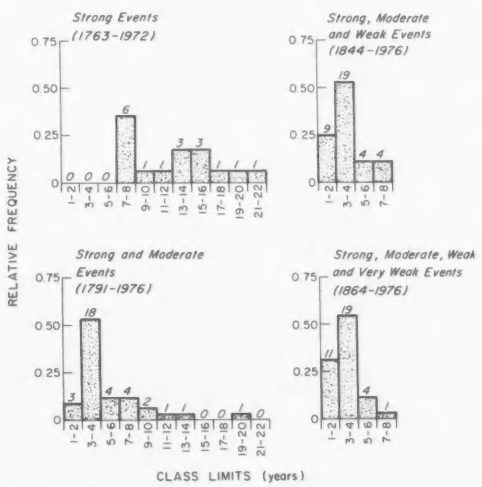

FIGURE 5.—Histograms of frequency distributions for El Niño type events by intensity. Number of occurrences within class intervals is indicated.

TABLE 2.—Strong El Niños, with intervals between events from onset to onset.

Onset year	Onset year	Years between onsets	Onset year	Onset year	Years between onsets
1763	1770	7	1884	1891	7
1770	1791	21	1891	1899	8
1791	1804	13	1899	1911	12
1804	1814	10	1911	1918	7
1814	1828	14	1918	1925	7
1828	1845	17	1925	1941	16
1845	1864	19	1941	1957	16
1864	1877	13	1957	1972	15
1877	1884	7			

209 (cumulative years between onsets) ÷ 17 (number of intervals) = 12.3 yr, average time interval between onsets of strong El Niños.

TABLE 3.—Strong and moderate El Niños with intervals between events from onset to onset.

Onset year	Onset year	Years between onsets	Onset year	Onset year	Years between onsets
1791	1804	13	1887	1891	4
1804	1814	10	1891	1896	5
1814	1817	3	1896	1899	3
1817	1819	2	1899	1902	3
1819	1821	2	1902	1905	3
1821	1824	3	1905	1911	6
1824	1828	4	1911	1914	3
1828	1832	4	1914	1918	4
1832	1837	5	1918	1925	7
1837	1845	8	1925	1929	4
1845	1864	19	1929	1939	10
1864	1868	4	1939	1941	2
1868	1871	3	1941	1953	12
1871	1877	6	1953	1957	4
1877	1880	3	1957	1965	8
1880	1884	4	1965	1972	7
1884	1887	3	1972	1976	4

185 (cumulative years between onsets) ÷ 34 (number of intervals) = 5.4 yr, average time interval between onsets.

TABLE 4.—Strong, moderate, and weak El Niños with intervals between events from onset to onset.

Onset year	Onset year	Years between onsets	Onset year	Onset year	Years between onsets
1844	1845	1	1905	1911	6
1845	1850	5	1911	1914	3
1850	1852	2	1914	1917	3
1852	1855	3	1917	1918	1
1855	1857	2	1918	1923	5
1857	1864	7	1923	1925	2
1864	1868	4	1925	1929	4
1868	1871	3	1929	1932	3
1871	1873	2	1932	1939	7
1873	1877	4	1939	1941	2
1877	1880	3	1941	1943	2
1880	1884	4	1943	1951	8
1884	1887	3	1951	1953	2
1887	1891	4	1953	1957	4
1891	1896	5	1957	1965	8
1896	1899	3	1965	1969	4
1899	1902	3	1969	1972	3
1902	1905	3	1972	1976	4

132 (cumulative years between onsets) ÷ 36 (number of intervals) = 3.7 yr, average time interval between onsets.

TABLE 5.—Strong, moderate, weak, and very weak El Niños with intervals between events from onset to onset.

Onset year	Onset year	Years between onsets	Onset year	Onset year	Years between onsets
1864	1868	4	1923	1925	2
1868	1871	3	1925	1929	4
1871	1873	2	1929	1932	3
1873	1875	2	1932	1939	7
1875	1877	2	1939	1941	2
1877	1880	3	1941	1943	2
1880	1884	4	1943	1946	3
1884	1887	3	1946	1948	2
1887	1891	4	1948	1951	3
1891	1896	5	1951	1953	2
1896	1899	3	1953	1957	4
1899	1902	3	1957	1963	6
1902	1905	3	1963	1965	2
1905	1911	6	1965	1969	4
1911	1914	3	1969	1972	3
1914	1917	3	1972	1975	3
1917	1918	1	1975	1976	1
1918	1923	5			

112 (cumulative years between onsets) ÷ 35 (number of intervals) = 3.2 yr, average time interval between onsets.

first mentioned in Quinn and Zopf (1975).] In some cases there was an initial fall from a large preevent (primary) peak which was not fully in phase with the seasonal relaxation (Southern Hemisphere summer and early fall) and the result was a relatively weak event; then, there was the rise to a smaller secondary peak followed by relaxation to a secondary trough which was in phase with the seasonal relaxation and resulted in a stronger event. The length of time between the two troughs was generally 18-22 mo and it is our opinion that situations of this type may account for many of the event-to-event intervals that fall in the short 1-2 yr category. Examples of such developments can be noted in 1950-53, 1962-65, and 1973-76 (Figure 2a, b). Preevent peaks occurred in 1950, 1962, and late 1973-early 1974. The first relaxation troughs following these peaks occurred in late 1951, late 1963, and late 1974-early 1975, and weak or very weak events resulted in all three cases. Then, there were rises to secondary peaks by mid-1952, mid-1964, and late 1975, followed by falls to troughs by early to mid-1953, mid-1965, and mid-1976, resulting in moderate El Niños for these latter years. We must be aware that these situations can arise and should be particularly wary when a large preevent peak is followed prematurely by a weak or very weak event. (One must not lose sight of the fact that these interannual fluctuations in the index anomaly trends were used to represent the interannual fluctuations in southeast trade and equatorial easterly strength as affected by the Southern Oscillation.) Figure 6 demonstrates the similarity of the three two-stage developments discussed above; a particularly obvious index trend was selected to represent each case.

The index trend between late 1872 and 1877 indicates a possible three stage development (Figure 3b), with a weak event in 1873, a very weak event in 1875, and a strong event in 1877 (Table 1). It is noteworthy that Indonesian droughts, which are usually associated with El Niño, occurred in 1873, 1875, and 1877 (Berlage 1957).

The preevent index anomaly peak has been reported to be a reliable indicator for subsequent El Niño type activity, and our long index record substantiates this viewpoint. We compiled statistics on the climb time from trough to peak and fall time from peak to trough from our long index anomaly record to provide some general guidance for event predictions. Figure 7 shows the applicable statistics. Events usually set in while the index is falling and prior to the index trough inflection point. Therefore, the contents of Table 6 and Figure 8, which pertain to time between index peak and subsequent event onset, can be used to further refine event predictions. We assumed a March onset time for all cases in arriving at values in the column headed "Peak to event onset" (Table 6). This assumption was made since month of onset was not available for most of the early cases, and a study of recent cases showed onset times to range from January to May.

INDONESIAN DROUGHTS

What happens over Indonesia relates to the Southern Oscillation (Berlage 1957) and is, therefore, an integral part of the activity affecting the

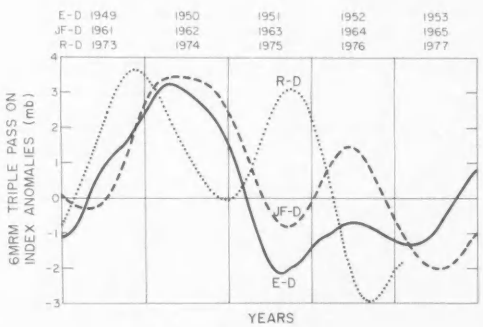

FIGURE 6.—Recent examples of two stage developments using triple 6-mo running mean plots of: 1) Easter-Darwin (E-D) index anomalies (1949-53); 2) Juan Fernandez-Darwin (JF-D) index anomalies (1961-65); 3) Rapa-Darwin (R-D) index anomalies (1973-77).

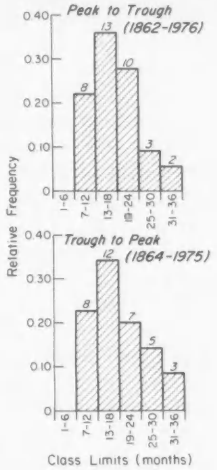

FIGURE 7.—Frequency distributions of rise time from trough to peak and fall time from peak to trough (in months) for the triple 6-mo running mean plots of Southern Oscillation index anomalies (see text). The number of cases falling within a class interval is entered at the top of the relevant histogram element.

equatorial Pacific and the oceanic region off northwestern South America. In general, years when the index is low and El Niño type activity occurs are also years of drought in Indonesia (particularly during the east monsoon season, May-October).

Using sea salt production on the Island of Madura (near Java), which is a very sensitive indicator of drought and precipitation, as well as some administration reports from Java estates, compiled by Van Bemmelen (1916), Berlage (1957) drew up a complete series of east monsoons drier than normal, from 1830 to 1953. Although 93% of the drought periods occurred during years when El Niño type events were under way (Table 7), only 77% of the periods when El Niño type events were underway were also designated as periods of east monsoon drought (Table 8). Nevertheless, the association between occurrences of these two phenomena and changes in the Southern Oscillation index trends are close enough in either case to indicate common relationships with the large-scale ocean-atmosphere changes over the Indo-

TABLE 6.—Time (in months) between index peak and El Niño type event onset (assuming onset is in March of indicated year), and time between index peak and associated Indonesian drought onset (assuming onset is in May of associated year). Pressure indices (see text) used to determine time of preevent peak were: S-B, Santiago-Bombay; S-D, Santiago-Darwin; JF-D, Juan Fernandez-Darwin; E-D, Easter-Darwin; T-D, Totegegie-Darwin; and R-D, Rapa-Darwin. In last column ND indicates no associated drought.

El Niño type event	Preevent index peak		Peak to event onset	Peak to drought onset
Year of onset	Month of peak	Index used	No. of Months	No. of months
1864	Aug.-Sept. 1862	S-B	18.5	20.5
1868	Mar.-Apr. 1867	S-B	11.5	ND
1871	Jan.-Feb. 1870	S-B	13.5	ND
1873	Jan. 1873	S-B	2.0	4.0
1875	Aug.-Sept. 1874	S-B	6.5	8.5
1877	Feb. 1876	S-B	13.0	15.0
1880	Nov. 1878	S-B	16.0	30.0
1884	May 1882	S-B	22.0	12.0
1887	July-Aug. 1886	S-B	7.5	21.5
1891	Nov.-Dec. 1889	S-B	15.5	17.5
1896	Oct. 1893	S-D	29.0	31.0
1899	Nov.-Dec. 1897	S-D	15.5	ND
1902	May 1901	S-D	10.0	12.0
1905	Sept.-Oct. 1903	S-D	14.5	16.5
1911	Jan.-Feb. 1910	S-D	13.5	ND
1914	Sept.-Oct. 1912	JF-D	17.5	7.5
1917	Aug.-Sept. 1916	S-B	6.5	ND
1918	Aug.-Sept. 1917	S-D	6.5	8.5
1923	Aug. 1921	JF-D	19.0	21.0
1925	May-June 1924	S-B	9.5	11.5
1929	Dec.-Jan. 1928/29	JF-D	2.5	4.5
1932	Aug.-Sept. 1931	S-D	6.5	8.5
1939	June-July 1938	JF-D	8.5	22.5
1941	Jan.-Feb. 1940	JF-D	13.5	15.5
1943	July-Aug. 1942	JF-D	7.5	21.5
1946	Dec.-Jan. 1944/45	S-B	14.5	4.5
1948	Aug. 1947	JF-D	7.0	ND
1951	Apr.-May 1950	E-D	10.5	ND
1953	Apr.-May 1952	R-D	10.5	12.5
1957	July-Aug. 1955	E-D	19.5	↑
1963	May 1962	JF-D	10.0	
1965	June 1964	JF-D	9.0	Data not
1969	Mar.-Apr. 1967	T-D	23.5	available
1972	Oct.-Nov. 1970	R-D	16.5	
1975	Nov.-Dec. 1973	R-D	15.5	↓
1976	Sept.-Oct. 1975	R-D	5.5	7.0

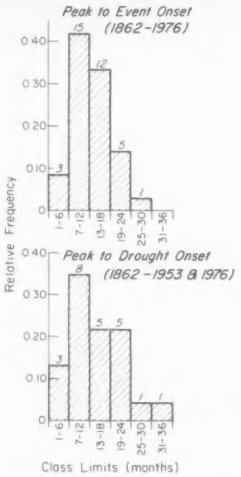

FIGURE 8.—Frequency distributions of time (in months) between preevent peaks in triple 6-mo running mean plots of Southern Oscillation index anomalies (see text) and: 1) the onset of subsequent El Niño type events (assuming onset is in March of involved years); 2) the onset of associated Indonesian droughts (assuming onset is in May of involved years). The number of cases falling within a class interval is entered at the top of the relevant histogram event.

Pacific region. Based on the association between El Niño type events, drought years and index features, and also an assumption that the drought will set in during May of involved drought years, we arrived at values in the column headed "Peak to drought onset" (Table 6). Figure 8 shows the resulting statistics which could be applied to Indonesian drought predictions.

TABLE 7.—Association of east monsoon droughts in Java with El Niño type events.

Drought years	El Niño type event years	Notes	Drought years	El Niño type event years	Notes
1844	1844		1913	1914	
1845	1845-46		1914		
1850	1850		1918	1918-19	
1853	None	Event in 1852	1919		
1855	1855		1923	1923	
1857	1857		1925	1925-26	
1864	1864		1926		
1873	1873		1929	1929-30	
1875	1875		1932	1932	
1877	1877-78		1935	None	Slight lowering of index
1881	1880	Index low 1880-81	1940	1939-40	
1883			1941	1941	
1884	1884-85		1944	1943-44	
1885			1945	1946	
1888	1887-89		1946		
1891	1891		1953	1953	
1896	1896		Drought data unavailable		1954-75
1902	1902		1976	1976	
1905	1905				

28 (separate events) ÷ 30 (east monsoon drought situations) = 0.93.

93% of east monsoon droughts can be associated with El Niño type events.

TABLE 8.—Association of El Niño type events with east monsoon droughts in Java.

El Niño type event years	Drought years	Notes	El Niño type event years	Drought years
1844	1844		1905	1905
1845-46	1845		1911-12	None
1850	1850		1914	1913-14
1852	None	Drought in 1853	1917	None
1855	1855		1918-19	1918-19
1857	1857		1923	1923
1864	1864		1925-26	1925-26
1868	None		1929-30	1929
1871	None		1932	1932
1873	1873		1939-40	1940
1875	1875		1941	1941
1877-78	1877		1943-44	1944
1880	1881	Index low 1880-81	1946	1945-46
1884-85	1883-85		1948	None
1887-89	1888		1951	None
1891	1891		1953	1953
1896	1896		Drought data unavailable	1954-75
1899-1900	None		1976	1976
1902	1902			

28 (east monsoon drought situations) ÷ 36 (separate events) = 0.78.

78% of El Niño type events can be associated with east monsoon droughts.

DISCUSSION

Over the past 116 yr (1861-1976), for which we have adequate data on the occurrence of El Niño type events of weaker intensity, there were decades of minimal activity (e.g., 1901-10, 1931-40, 1961-70), but no decade without such activity. There is no reason to expect any significant change in the amount of El Niño activity in the foreseeable future over that experienced in the past century. Therefore, it would appear that our data (e.g., Tables 2-5) might eventually be used in conjunction with associated catch data and biological findings for effective long-range planning in the management of the anchoveta fishery. For example, assessment of maximum sustainable yields under various environmental conditions ranging from the favorable extended anti-El Niño condition (when there are two or more consecutive years with high Southern Oscillation indices) to the El Niño situation (when there are rapidly falling and low Southern Oscillation indices) might prove useful for determining the optimum size and flexibility of the fishing fleet and fish processing facilities. A key element to such assessments will be a knowledge of the required biological recuperation time following cessation of an unfavorable physical environmental condition.

Such data could also be used for speculative long-range outlooks. For example, if we had just experienced a strong El Niño, our results suggest that there is a near-zero probability that we would experience another strong event in <7 yr after the onset of the recent situation. However, there would be an 86% probability that an event in the very weak, weak, or moderate category would occur within 3-4 yr after the strong El Niño onset. Considering the current situation, and recognizing that a moderate event set in during 1976 and held over into early 1977, there is a 54% probability (based on our data) that another event of unknown intensity would set in during 1980. It would not be reasonable to go beyond statistical estimates until we find we are approaching a peak in the Southern Oscillation index anomalies.

When we are nearing a preevent peak and can assess its height and time of occurrence, then we can use peak to trough statistics (e.g., Figure 7) to advantage in forecasting onset time and likely intensity of the coming El Niño type event. The intensity would be based on the height of the index anomaly peak and the time of year when the subsequent trough was expected to occur. Event onset time can be further refined by considering Figure 8 statistics. It is also essential in the prediction procedure to realize that some developments may involve two or more stages. In cases of this type, forecast lead times for the separate stages will often be greatly reduced (to 1-6 mo in advance), unless historical analogies lead to pattern recognition as the situation evolves.

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THE PRECISION OF SIMULATED TRANSECT SURVEYS OF NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, SCHOOL GROUPS

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ABSTRACT

Simulated transect surveys of model anchovy populations were compared in terms of precision and efficiency. The precision of systematic surveys varies inversely with the distance between transects. Systematic surveys give more precise population estimates than random surveys, due to the large positive correlation between closely spaced transects. The precision of stratified systematic surveys is not significantly different from that of the unstratified surveys when the school groups are randomly distributed in the survey area. However, stratified systematic surveys are more precise when the school groups are clumped in one end of the survey area. The results of the simulations show that the patchy distribution of anchovy schools can be a major source of error in population estimates.

Any sampling program intended to estimate the size of a population is subject to a variety of errors which may reduce the accuracy or precision of the estimate. Precision is the reciprocal of the variation of replicate estimates. Successful management of a northern anchovy fishery in California will require the monitoring of changes in the population size. Acoustic survey techniques are currently being developed to obtain population and biomass estimates independent of the fishery (Hewitt et al. 1976). As in the study of any biological population, it will be important to avoid confusing the variation of a series of estimates due to sampling error with true fluctuations in the population size.

Precision may be affected by 1) the manner in which the sampled population is distributed in space, and 2) variations within the sampling method itself. Several studies have shown that the patchy distribution of individuals in a population may cause considerable variation in replicate population estimates and that the variation is related to sample design. Winsor and Clarke (1940) studied the variation of catches in series of plankton net tows. Although they did not separate the components of between-tow variation due to factors (1) and (2), it was observed that oblique tows were more precise than vertical or horizontal tows. Barnes and Marshall (1951) took an extensive series of replicate pump samples and attributed the considerable variation observed to the nonrandom distribution of the zooplankton since the volumes filtered were known accurately. Taft (1960) analyzed the variance of sardine egg counts in a grid of closely spaced stations. The distribution of eggs was extremely patchy (the densities between samples ranged over more than four orders of magnitude) and the relative 95% confidence limits for an estimate of the egg population in the area of the grid from a single sample were represented by a factor of 62. A simulation study by Wiebe (1971) showed that the precision of zooplankton population estimates depends both on the sampling design (net size and tow length) and the distribution of the population (size and location of patches).

Similar studies have investigated the precision of sampling fish populations. Taylor (1953) discussed the implications of the patchy distribution of fish for the optimum design of trawl surveys to estimate population size. Cram and Hampton (1976) demonstrated that the patchy distribution of pilchard schools can cause imprecision sufficient to render a population estimate useless for management.

The anchovy population is patchy on two levels: individual fish are aggregated in schools and schools themselves tend to be aggregated in school groups. This patchiness, or nonrandomness, is expected to be a major source of variation in population estimates. The present study simulated surveys of model anchovy populations to determine the effect of patchiness on the precision of population estimates. Three transect survey designs were compared: systematic, random, and stratified systematic. These are merely different

[1]Scripps Institution of Oceanography, University of California, San Diego, La Jolla, CA 92093.

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methods of selecting transects, or allocating sampling effort. The three types of simulated survey, with a range of sample sizes (numbers of transects), were run on 15 model anchovy populations.

METHODS

Anchovy populations were modeled as arrays with each element representing 1 n.mi.^{2}. The array dimensions were 180 × 75, approximately the dimensions, in miles, of the Los Angeles Bight. Since a school is the population unit detected in an acoustic or aerial survey, the units of the model populations were schools. One hundred fifty thousand schools were distributed in the array resulting in a mean density of 11.1 schools/mi^2. Four acoustic surveys by the California Department of Fish and Game[2] in 1975 and 1976 yielded estimates ranging from 88,887 to 319,878 anchovy schools off southern California in the area of the bight. Mais (1974) gave a range of 21,920-343,070 ($\bar{x}$ = 150,996) schools off southern California and northern Baja California, most of which were within the bight.

The schools were placed in circular school groups located at random. Schools were distributed uniformly within a school group. School group radii and densities were chosen randomly and independently from log-normal approximations of observed frequency distributions based on 52 school groups from six California Department of Fish and Game Sea Survey acoustic surveys (MacCall et al.[3]) (Figure 1). There was no significant correlation between the density of schools within a school group and the size of the school group in these observations. Where school groups overlapped, the densities were simply added together, although this effectively increased both the mean radius and density. In one model population illustrated in Figure 2, 16 school groups containing 150,303 schools covered about 14% of the survey area. Fifteen model populations were used, each with the same total number of schools, but different locations, sizes, and densities of school groups.

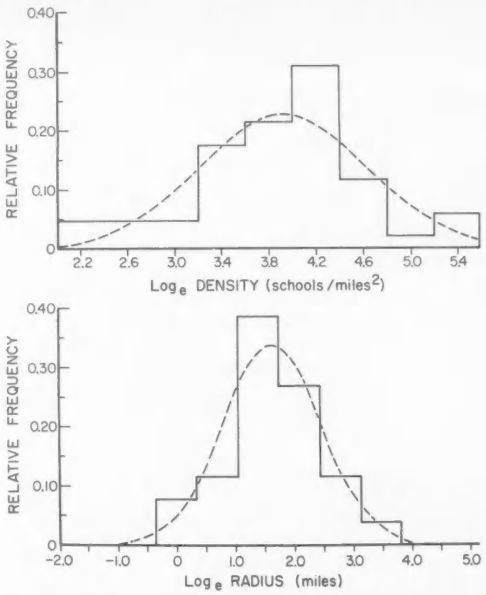

FIGURE 1.—Comparison of distributions of northern anchovy school group density and size observed in the California Current during California Department Fish and Game surveys (solid lines) to log-normal approximations used in simulations (dashed lines).

A simulated survey consisted of a series of transects across the survey area. There were 180 possible transects, each 1 mi wide. Acoustic surveys currently run by the Southwest Fisheries Center, National Marine Fisheries Service, NOAA, used a transect width of 0.14 mi (250 m). Aerial transect widths were typically 0.2 to 0.5 mi. A larger transect width was used in the simulations to hold the model population array down to a reasonable size. We assumed that the general results of the simulations would not change by using a smaller transect width. Since all schools were counted within a transect, the only source of error in the survey estimate was the large variance in the number of schools per transect. For instance, in the model population in Figure 2, the mean number of schools per transect was 835.0, while SD was 920.4 (variance = 8.47 $\times 10^5$).

Systematic surveys were simulated by counting the schools within a series of transects separated by a constant transect interval. A population estimate was calculated simply by dividing the survey count by the fraction of the survey area covered by the transects. Transect intervals of 2, 3,

[2]S. J. Crooke. 1975. Cruise reports 75-A-1 and 75-A-6. K. F. Mais. 1976. Cruise reports 76-A-3 and 76-A-9. State of California - The Resources Agency, Department of Fish and Game, Marine Resources Region, Long Beach, CA 90802.

[3]MacCall, A., P. E. Smith, G. Stauffer, J. Squire, J. Zweifel, and S. Crooke. Report of CalCOFI anchovy workshop working group on methods of estimating anchovy abundance. Unpubl. manuscr. Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, CA 92038.

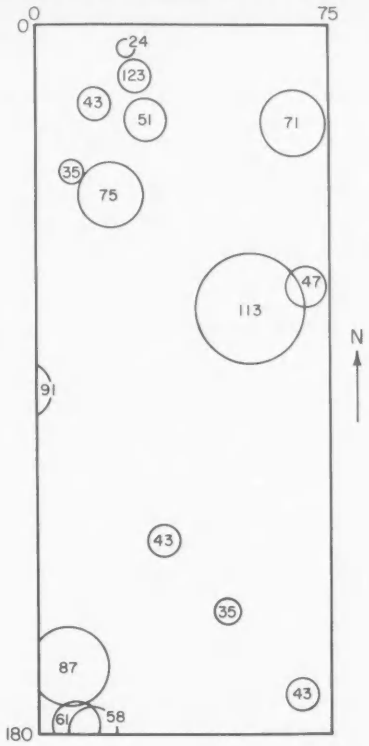

FIGURE 2.—A model northern anchovy population. Densities of school groups in schools per square mile. Simulated survey transects are oriented horizontally. The numbers on the axes are the coordinates of the array and the dimensions, in miles, of the survey area it represents.

4, 5, 7, 10, 12, 15, 20, 25, 30, and 40 mi were used. A survey with a transect interval of d miles consisted of $180/d$ transects. For each transect interval, 20 replicate surveys were run by randomly choosing the initial transect from the first d transects in the survey area. The replicate survey estimates were used to calculate an unbiased mean population estimate and a coefficient of variation (standard deviation of the replicate estimates divided by the mean), which is a measure of the precision of the estimate (Wiebe 1971). This procedure was repeated on the 15 different model populations.

Random surveys were simluated in an analogous manner to allow a direct comparison of sampling errors. For each of the transect intervals (d) of the systematic surveys, 20 replicate surveys were run consisting of $180/d$ transects chosen at random without replacement (a transect was not repeated within a survey). Coefficients of variation were calculated as a measure of precision.

Stratified systematic surveys were simulated after dividing each of the model populations into four 45-mi wide strata. The schools along three transects in each of the four strata were counted to obtain a preliminary estimate of relative population sizes. Then a total of 60, 36, 18, 12, 9, 7, or 6 transects were divided among the strata according to the estimated population fractions. For example, if a stratum contained one-half of the schools counted in the preliminary survey, one-half of the total number of transects was allocated to that stratum for the stratified survey. At least one transect was allocated to each stratum to avoid biasing the final population estimate. For each total number of transects, 20 replicate systematic surveys were run by randomly choosing the initial transect and simulating a systematic survey within each stratum with the allocated number of transects. Once again, coefficients of variation of the replicate population estimates were calculated for each of the 15 model populations.

RESULTS

The results of the systematic survey simulations indicate that the sampling error represented

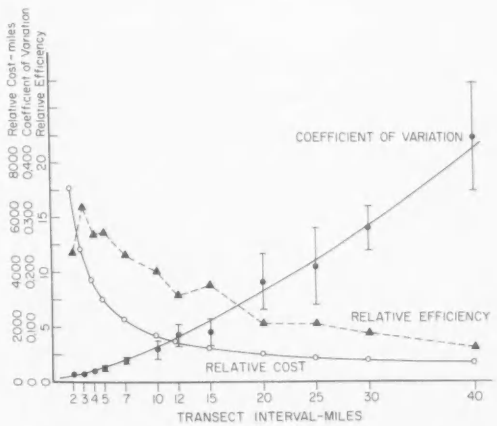

FIGURE 3.—Results of the simulations of systematic surveys of the 15 models for northern anchovy populations. Relative efficiency is proportional to precision (the reciprocal of the coefficient of variation) divided by relative cost (see text). Averages and 95% confidence limits are given for coefficients of variation.

by the coefficient of variation increased as the transect interval increased and sample size decreased (Figure 3). The cost of a survey was assumed to be proportional to the distance covered along the transects plus 360 mi to and from port. Relative efficiency was 10^3 times the reciprocal of the product of the coefficient of variation (C.V.) and relative cost, i.e., precision divided by cost. Efficiency generally decreased as the transect interval increased, but peak efficiency was obtained at a transect interval of 3 mi. By interpolation, it can be seen that a population estimate may range 10 and 25% ($2 \times$ C.V.) from the true population size when surveys are run with transect intervals of 8.5 and 16 mi, respectively.

Systematic sampling gave a consistently lower coefficient of variation, or greater precision than random sampling (Figure 4). The variability between model populations, indicated by the confidence limits on the mean coefficient of variation, was greater for the random sampling error ($F_{(14,14)} \geq 5.44, P<0.05/12$) for 8 of the 12 sample sizes. Also represented in Figure 4 are the expected coefficients of variation for random sampling calculated from the model population parameters (σ^2 and μ) by the following equation with a finite population correction:

$$\text{C.V.} = \frac{1}{\mu}\sqrt{\frac{\sigma^2}{n}\left(\frac{N-n}{N}\right)}$$

where σ^2 = the average variance of the number of schools per transect in the 15 model populations = 1,154,636

μ = the mean number of schools per transect = 835.3

n = the number of transects in the survey

N = total number of transects in the survey area = 180.

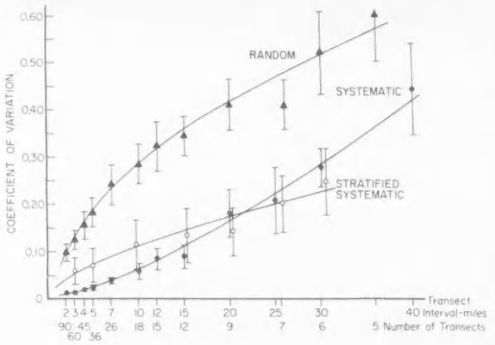

FIGURE 4.—Comparison of the results of the simulations of random, systematic, and stratified systematic surveys. For random surveys, the curve represents the expected coefficients of variation calculated from the parametric variance of the model populations (see text).

For 11 of the 12 sample sizes, the expected value was within 95% confidence limits of the mean observed coefficient of variation. This close agreement supports the validity of the method used to obtain the coefficients of variation in the simulations. There was apparently no significant difference between the coefficients of variation of the systematic and stratified systematic surveys (Figure 4). This was confirmed by analysis of variance (Table 1, $P>0.25$ that there was no added variance due to survey design). However, there were significant interaction effects between survey design and model population ($P<0.01$ that there was no added variance from this source) and between survey design and the number of transects ($P<0.05$).

An attempt was made to elucidate the interactions involving survey design by performing analyses of variance on subsets of the data. It was found that for large sample sizes (transect interval $\leq$15 mi, or number of transects $\geq$12) unstratified

TABLE 1.—Analysis of variance of the coefficients of variation from simulated systematic and stratified systematic surveys of model northern anchovy populations. This is a mixed model analysis of variance (Sokal and Rohlf 1969): survey design and number of transects are fixed treatment effects and model population is a random effect.

Source of variation	SS	df	MS	Significance level
Main effects:				
Survey design	0.0157	1	0.0157	$F_{(1,14)} = 0.908$, $P>0.25$
Number of transects	1.2872	6	0.2145	$F_{(6,84)} = 56.681$, $P<<0.001$
Model population	0.5270	14	0.0376	$F_{(14,84)} = 8.000$, $P<0.001$
Interactions:				
Design-number of transects	0.0748	6	0.0125	$F_{(6,84)} = 2.627$, $P<0.05$
Design-population	0.2418	14	0.0173	$F_{(14,84)} = 3.681$, $P<0.001$
Number of transects-population	0.3179	84	0.0038	$F_{(84,84)} = 0.819$, $P>0.50$
Error	0.3988	84	0.0047	
Total	2.8633	209		

systematic surveys were significantly more precise than stratified systematic surveys ($P<0.025$), although there is still a significant interaction between survey design and model population ($P<0.001$). For smaller sample sizes, there was no significant difference between the precision of the two designs.

In the model populations, school groups were located randomly within the survey area. However, the distribution of schools between strata was never random because of the wide range of school group sizes and the small number of school groups in a population. The 15 model populations were divided into three groups (low, intermediate, and high nonrandomness) based on the index of dispersion of the number of schools per stratum. Analysis of variance revealed that for highly nonrandom populations, stratified systematic surveys were significantly more precise than unstratified surveys ($P<0.025$). On the other hand, there was no significant difference between the survey designs for populations of intermediate or low nonrandomness. The effect of the nonrandomness of the populations, in the limited sense used here, is illustrated more dramatically below.

In summary, these results indicate that both the number of transects and the spatial distribution of the population can affect the precision of a survey estimate. The effect of survey design involves complex interactions with the other two factors. These factors should be considered, if possible, when choosing the optimum design for a survey.

DISCUSSION

In general, systematic sampling may result in considerable gains or losses in precision compared with simple random sampling. The greatest increase in precision occurs when there is a high degree of correlation between adjacent sampling units and the correlation decreases as the interval between units increases. In this situation, systematic sampling resembles stratified sampling. On the other hand, precision may be greatly reduced when there is a periodic variation in the population and the sampling interval is equal to this period or a multiple of it (Hansen et al. 1953).

Correlograms between sampling units (transects) in five of the model anchovy populations indicated that transects <10 mi apart had a high positive correlation, while the correlation tended to be slightly negative at distances >20 mi (Figure 5). This autocorrelation structure was due to the frequency distribution of school group sizes. The mean distance at which the autocorrelation function passed through zero was 15.0 mi, while the mean diameter of the individual school groups in the five model populations was 11.8 mi. Distribution of school groups within the model populations was random. However, real populations are likely to be nonrandom in this respect and additional correlations would be expected from this factor. The strong positive correlation between transects separated by short distances explains why systematic surveys with small transect intervals were more precise than random surveys with an equivalent number of transects. As the transect interval increased, the correlation between transects decreased to near zero and the imprecision of systematic sampling approached that of random sampling (Figure 4).

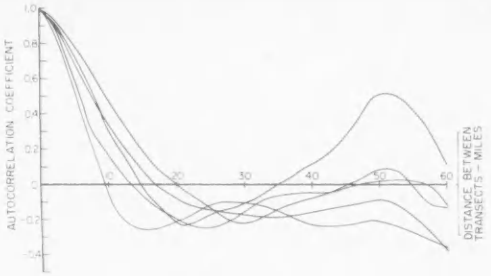

FIGURE 5.—Autocorrelation of transect counts in five model northern anchovy populations.

In order to reduce total sampling error, a common strategy is to allocate effort proportional to the sampling error within parts of a sampling program. The variation observed in the population estimates of the simulated surveys was caused by the large variance in the number of schools per transect. It can be shown in the model populations, as in many biological populations, that the standard deviation was positively correlated with the mean number of schools per transect in a stratum. Therefore, it was thought that the stratified systematic surveys would reduce the total sampling error by allocating more transects where the variance was large. The simulations failed to show any gains in precision from this strategy. This result was not expected, but is possibly due to the random distribution of school groups. The model populations may have been ideal in this sense, but we had relatively little information on the distribution of school groups within the range of the

northern anchovy. As stated above, stratified systematic surveys were significantly more precise than unstratified surveys for the five model populations with the most nonrandom distribution of schools between strata. If the school groups themselves are aggregated, it is reasonable to expect an increase in precision by stratifying the survey.

To test this possibility, the simulations were repeated on model populations in which the school groups were limited to only one-half of the survey area. An analysis of variance (Table 2) indicated in this case that the stratified systematic surveys were more precise than the unstratified systematic surveys ($P<0.005$ that there was no added variance due to survey design). The overall mean coefficients of variation were 0.095 and 0.133, respectively. However, there were significant interaction effects involving survey design, indicating that the advantage of stratifying the survey will depend on the number of transects and the spatial distribution of the population. The additional cost of the preliminary survey in the stratified design must also be considered when comparing it with the unstratified design.

The results of the simulated systematic surveys showed that the patchy distribution of schools was an important source of error in estimates of the anchovy population size. Acoustic surveys run by the Southwest Fisheries Center have used transect intervals of 6.6 and 40 mi. The simulations gave evidence that the population estimates from these surveys could be expected to range at least 8 and 90% (2 × C.V.), respectively, from the true population size. The most efficient simulated sampling, in terms of precision per unit cost, occurred at a transect interval of 3 mi. This would require a cruise grid of 4,860 mi, equivalent to a 34-day acoustic survey at 12 kn and 12 h per day, to reduce the coefficient of variation (due to the patchy distribution of schools) to 1.4%. Maximizing efficiency is not a valid goal, however, when the precision gained is greater than that required for the problem of managing the fishery, when other sources of error become more important, and when there are absolute limits on cost. Anchovy population estimates within 25% of the true value might be considered sufficient for management, at least to allow confidence that a consistent change observed over several years is real (pers. commun., P. E. Smith, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, Calif., Oct. 1977).

As stated before, the anchovy population is patchy on two levels: individuals are aggregated into schools and schools are aggregated into school groups. The simulations have quantified the sampling error due to the second level of patchiness only. Although little is known about the distribution of anchovy school groups, it was also demonstrated that their aggregation is potentially an important consideration in designing a survey. The acoustic survey methods currently used by the National Marine Fisheries Service and the California Department of Fish and Game do little more than count the number of anchovy schools (Hewitt et al. 1976; Mais 1974). The Department of Fish and Game calculates a biomass estimate by multiplying the observed school area by a constant factor thought to represent an average biomass per unit area. More sophisticated methods of estimating biomass from the acoustic signal received from a school are now being explored at the Southwest Fisheries Center. For these reasons, the problem of sampling error due to a varying number of fish per school (the first level of patchiness) was not addressed here.

Many sources of error may be involved in an anchovy biomass estimate. Patchiness is important in any type of sampling program. Other sources of error that may be important in an

TABLE 2.—Analysis of variance of the coefficients of variation from simulated systematic and stratified systematic surveys of model northern anchovy populations when the model population school groups are clumped in one-half of the survey area.

Source of variation	SS	df	MS	Significance level
Main effects:				
Survey design	0.0732	1	0.0732	$F_{(1,14)} = 12.908$, $P<0.005$
Number of transects	1.4995	6	0.2499	$F_{(6,84)} = 119.403$, $P<<0.001$
Model population	0.1327	14	0.0095	$F_{(14,84)} = 4.318$, $P<0.001$
Interactions:				
Design-number of transects	0.0476	6	0.0079	$F_{(6,84)} = 3.589$, $P<0.005$
Design-population	0.0794	14	0.0057	$F_{(14,84)} = 2.591$, $P< 0.01$
Number of transects-population	0.1758	84	0.0021	$F_{(84,84)} = 0.955$, $P>0.50$
Error	0.1858	84	0.0022	
Total	2.1941	209		

acoustic survey are as follows (Instituto del Mar del Peru 1974; Cram and Hampton 1976; P. E. Smith pers. commun.):

1) Failure to discriminate between anchovy schools and other acoustic targets.
2) Unschooled fish and small schools not detected.
3) Vessel avoidance.
4) Inability to survey in shallow inshore waters.
5) Movement of school groups relative to the survey grid.
6) Fish in the top surface layer missed by the acoustic beam.
7) Errors in the factor for conversion of the acoustic signal information to a biomass estimate.
8) Effect of varying hydrographic conditions on the acoustic signal.
9) Blocking of signal to and from fish far from the ship by fish nearer to the ship.

The magnitude of the error caused by these factors can now only be roughly estimated. They may affect either or both the precision and accuracy of a population estimate. Corrections to reduce the biases are conceivable. The present study has demonstrated the magnitude of the error associated with the patchiness of the anchovy population. Although the model population distributions may be crude approximations to the real distribution, the general conclusions reached here are not likely to be changed by adding further levels of complexity to the model. The sampling error due to patchiness can be reduced by properly designing a survey, but never eliminated. Temporal and spatial differences in population estimates must be interpreted with an awareness that the error exists.

ACKNOWLEDGMENTS

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INTERSEX ANOMALIES IN SHRIMP OF THE GENUS *PENAEOPSIS* (CRUSTACEA: PENAEIDAE)

While examining a relatively large collection of *Penaeopsis* (40 lots containing 196 specimens) taken by the U.S. steamer *Albatross* during the Philippine Expedition, 1907-10, I found three specimens having external characteristics of both males and females. Each specimen had a fully developed thelycum, a moderately well-developed petasma (about two-thirds the length of the petasma of males of corresponding size), small appendices masculinae, and genital apertures on the coxae of the fifth pair of pereopods. The shrimps were poorly preserved—the exoskeletons were soft, rostrums and telsons broken, and internal organs macerated; however, most of the features of the carapace were clearly distinct and the external genitalia intact.

The discovery of these shrimp elicits several questions: to which species do they belong? What is their functional sex? Do they represent a transitional stage in a protandrous hermaphroditic species? If not, have their intersex-appearing anomalies resulted from parasitism? Although none of these questions is answered definitively, all are discussed following a brief description of the external genitalia of the shrimp.

The specimens are deposited at the National Museum of Natural History: USNM 170581, 23 mm cl (carapace length), Bohol Strait, between Bohol and Cebu, 291 m, 25 March 1909, *Albatross* stn 5418. USNM 170582, 24.5 mm cl, Bohol Strait, 320 m, 25 March 1909, *Albatross* stn 5419. USNM 170583, 19 mm cl, Gulf of Davao, SE Mindanao, 247 m, 18 May 1908, *Albatross* stn 5247.

Description

Petasma (Figure 1B-C) with length about two-thirds that of petasma of males of *P. rectacuta* of comparable size, and twice as long as endopod of first pair of pleopods in females of *P. rectacuta* (Figure 1A) and all other congeners. Dorsomedian lobule with distinct distomedian projection and well-formed proximal plate. Dorsolateral lobule with supporting rib (in two of three specimens) ending proximally in subelliptical process. Ventral costa tapering distally, forming free, inwardly excavate, blunt projection directed dorsomesially at broadly obtuse angle with shaft of petasma.

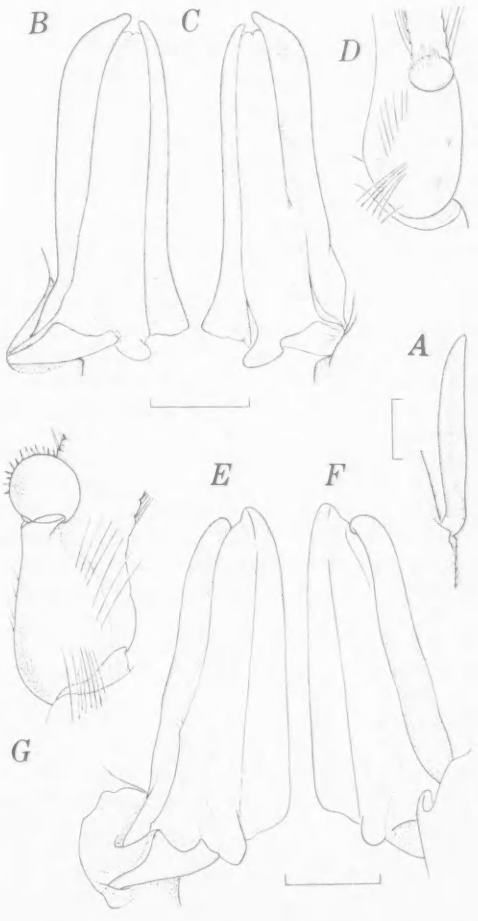

FIGURE 1.—A, *Penaeopsis rectacuta*, USNM 170586, ♀ 23.5 mm cl (carapace length), off Palompon, Leyte, Philippines, endopod of left first pereopod, dorsal view. B, *Penaeopsis* sp, USNM 170582, 24.5 mm cl, Bohol Strait, Philippines, *Albatross* stn 5419, petasma, dorsal view of left half. C, Ventral view of same. D, Left appendix masculina, dorsal view, same specimen. E, *Penaeopsis rectacuta*, USNM 170587, ♂ 13 mm cl, off Mindanao, Philippines, *Albatross* stn 5518, petasma, dorsal view of left half. F, Ventral view of same. G, Right appendix masculina, dorsal view, same specimen. 0.5 mm indicated.

Appendix masculina (Figure 1D) minute, somewhat oval, bearing distal patch of setae; thickening at its base, inconspicuous.

Thelycum (Figure 2A-C) with anterolateral borders of plate of sternite XIV varying from slightly concave to convex, and separated by posteromedian projection of sternite XIII; plate strongly slanting dorsomesially, its surface flat or each side biconvex ventrally. Lateral borders slightly concave, strongly converging posteriorly, not reaching posterior ridge but separated from it by deep depression, latter extending anteriorly adjacent to median rib and merging with anteromedian depression; median rib broadest basally, gently tapering toward, but not reaching, posteromedian projection of sternite XIII. Median plate of XIII trilobed to cordiform, slightly to pronouncedly elongate, covered with setae (most lost in specimen illustrated in Figure 2C) except for naked central concavity, setae directed anteriorly except on base of posteromedian projection where directed caudally; posteromedian projection short, with caudal margin straight or shallowly emarginate. Sternite XII bearing small posteromedian tooth and pair of sharp ridges, extending posterolaterally from base of tooth.

Discussion

In several features the three specimens are markedly similar to members of *P. rectacuta* (Bate 1881). The rostrum (Figure 3) is straight and its second tooth is located in line with the orbital margin, the anteroventral angle of the carapace is approximately 90°, and the moderately long branchiocardiac carina is conspicuous, its anterior extremity not nearly reaching the posterior end of the hepatic sulcus. Also the relative length of the pereopods and—in the two smaller animals—the shape of the median plate of sternite XIII are similar to those in *P. rectacuta*. Furthermore, the three shrimps were collected together with specimens of the latter species, all three in localities where the only other *Penaeopsis* occurring in the area (*P. eduardoi* Pérez Farfante 1977) was not taken—another indication that these shrimp probably belong to *P. rectacuta*.

The petasma and the thelycum of these shrimp are different from those of other species of *Penaeopsis*, including those of *P. rectacuta*. The ventral costae of the petasma (Figure 1B-C), tapering distally into a short projection disposed at an obtuse angle to the shaft, differ from those of adult males of *P. rectacuta* in which the ventral costae turn abruptly at right angles and bear a thin marginal border that is bent inward. In the three specimens the petasma somewhat resembles that of large juveniles (with a carapace length of about 13 mm) of *P. rectacuta* (Figure 1E-F); however, in the latter the distomedian projections are less distinct than they are in my specimens or in adult *P. rectacuta*. Also, in juveniles of *P. rectacuta* the ventral costae do not taper distally into free projections, instead the tips are broad and turned

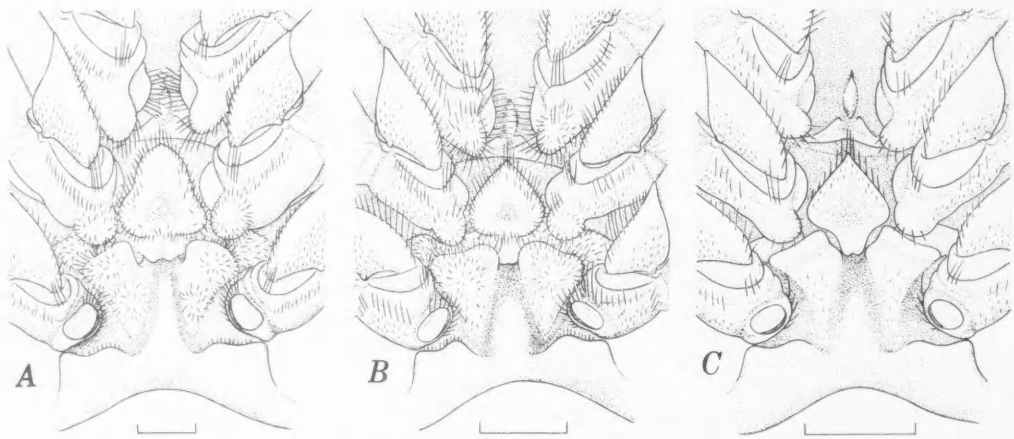

FIGURE 2.—*Penaeopsis* sp. Thelyca. A, USNM 170582, 24.5 mm cl, Bohol Strait, *Albatross* stn 5419. B, USNM 170581, 23 mm cl, Bohol Strait, *Albatross* stn 5418. C, USNM 170580, 19 mm cl, Gulf of Davao, Mindanao, Philippines, *Albatross* stn 5247. 2 mm indicated.

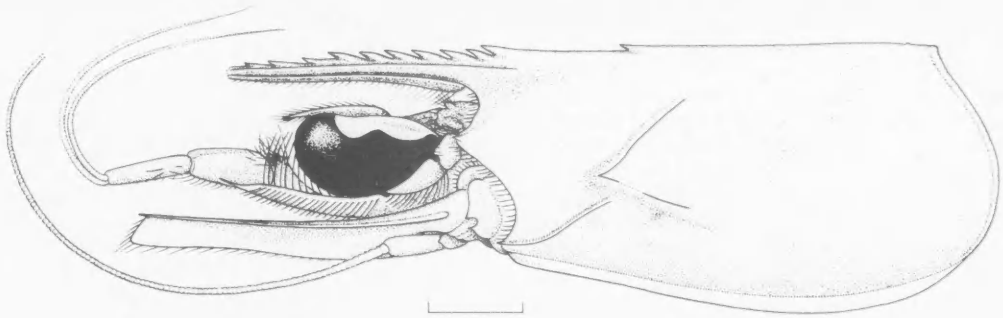

FIGURE 3.—*Penaeopsis* sp, USNM 170582, 24.5 mm cl, Bohol Strait, Philippines, *Albatross* stn 5419. Cephalothorax, lateral view. 5 mm indicated.

at right angles to the shaft. The appendices masculinae (Figure 1D) are considerably less well developed in the present specimens than in juvenile males of *P. rectacuta*, in which they are circular (Figure 1G), and bear only marginal setae. The thelyca of the three specimens differ from those of *P. rectacuta* in that the lateral borders of the plate of sternite XIV converge strongly (rather than gradually) toward the posterior thoracic ridge and are separated from the ridge by a deep groove, a unique characteristic; the median plate of sternite XIII, although trilobed in one specimen, is cordiform in the other two, the latter resembling that of *P. rectacuta*.

The functional sex of the three specimens cannot be ascertained because their gonads had disintegrated. It is unlikely that they were hermaphrodites for each bears only one pair of gonopores. Because they have a completely developed thelycum one would expect ovipores to occur on the coxae of the third pair of pereopods, but whereas these coxae are similar in outline to those of female *P. rectacuta*, they lack openings and are covered by a hardened cuticle (Figure 2A-C) like those of males; instead, the coxae of the fifth pair of pereopods exhibit a membraneous cuticle with an opening on the proximomesial border. Although the latter aperture is situated on the last pereopod, it occurs on the coxa (Figure 4A) rather than on the bulging articular membrane as it does in typical males (Figure 4B). Furthermore, no terminal ampullae—the ectal muscular region of the vasa deferentia—appear to have been present, even though the skeletal muscles are rather well preserved.

Many anomalies of the secondary sexual characters of decapod crustaceans have been recorded, e.g. in lobsters (Chace and Moore 1959, among others) and crayfishes (Turner 1924, 1929, 1935). Recently Zongker (1961) described many sexually aberrant individuals within a population of *Cambarus montanus acuminatus* Faxon 1884. Among the aberrant individuals she found were females (sex identified by examination of the gonads) lacking ovipores on the coxae of the third pair of pereopods, but with "male openings" on those of the fifth, an anomaly similar to that exhibited by my specimens. In these shrimp, the apertures are not typical of penaeoid males because of their location on the coxae rather than on the articular membranes. Being present on the coxae, they resemble female openings; however, ovipores are typically subcircular rather than slitlike and, furthermore, they are characteristically situated on the mesial surface of the coxa, dorsal to the coxal plate, instead of on the ventral face as in my specimens.

Individuals of the superfamily Penaeoidea bearing both a thelycum and a petasma have not been recorded previously in the literature. Based on size distribution and characters of the endopod of the first pair of pleopods in females, Heegaard (1967, 1971, 1972) suggested the possibility that protandrous hermaphroditism occurs in *Solenocera membranacea* (Risso 1816) and also in *Penaeus kerathurus* (Forskål 1977), but no individuals with both petasma and thelycum were found by him. The external genitalia in my three specimens causes one to suspect that they might be transitional forms and that therefore at least some members of the genus *Penaeopsis* exhibit protandrous hermaphroditism (protandrous because at their size the thelyca are fully developed whereas the petasmata are relatively small). Their rather

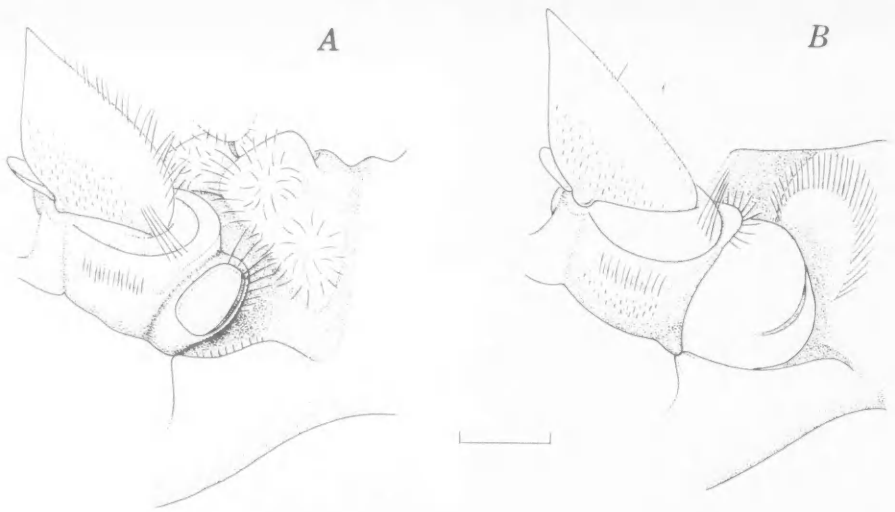

FIGURE 4.—Right fifth pereopod. A, *Penaeopsis* sp, USNM 170582, 24.5 mm cl, Bohol Strait, Philippines, *Albatross* stn 5419. B, *Penaeopsis rectacuta*, USNM 170586, ♂ 24.5 mm cl, off Palompon, Leyte, Philippines, *Albatross* stn 5403. 1 mm indicated.

large size, however, makes it unlikely that they are in a transitional stage. Furthermore, hermaphroditism has not been recorded in any species of the genus *Penaeopsis*, consequently its occurrence in these specimens would be exceptional.

Effects of parasitism in a species of *Metapenaeopsis*, a genus closely allied to *Penaeopsis*, were reported by Hiraiwa and Sato (1939). These authors observed conspicuous changes in the petasmata of males and the gonopores of males and females in the shrimp *Penaeopsis akayebi* Rathbun 1902 (= *Metapenaeopsis barbata* de Haan 1850) parasitized by the bopyrid isopod *Epipenaeon japonica* Thielemann 1910. In males, the petasmata were considerably smaller than those in normal individuals of corresponding size and their two parts were unjoined; the gonopores were barely noticeable, and the papillae, at the tips of which the gonopores are situated in normal individuals, were lacking. In the females, the ovipores were obscured, but the thelycum was not apparently affected by the presence of the parasite. In the extensive material examined, however, none of the specimens bore both a petasma and a thelycum. Among the specimens of *P. rectacuta* collected in the waters of the Phillippines, I found a few that were parasitized by bopyrids (one of them was taken at Bohol Strait, in a locality near those at which two of my three individuals were obtained). The parasitized specimens had normal external genitalia, thus lending no support to an assumption that the anomalies in the genitalia of these three individuals were induced by a bopyrid parasite. Nevertheless, parasitism offers the only clue as to the possible origin of the anomalies present in these shrimp.

Acknowledgments

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ON THE ROLE OF THE DIFFERENT FIBRE TYPES IN FISH MYOTOMES AT INTERMEDIATE SWIMMING SPEEDS

In most fishes the myotomal locomotor musculature is made up of two main fibre types: a superficial layer of red fibres overlies the white fibres which form the main mass of the myotome. A spectrum of such differences as mitochondrial content, enzyme activities, blood supply, and innervation (as well as color) distinguishes these two fibre types.The electrophysiogical properties of the two fibre types have only been investigated in a few species, but in all of these the white fibres have been found to propagate muscle action potential, whereas only local nonpropagated activity is seen from red fibres (which are invariably multiply innervated). In many (but not all) fishes, there are also other less abundant fibre types in the myotomes, in some respects intermediate between the red and the white fibres (e.g., Patterson et al. 1975).

There is general agreement that at low sustained swimming speeds only the red fibres are employed and that the white fibres are active during short bursts of maximum speed, which cannot be long sustained. However, agreement has not yet been reached about which fibres are active during sustained swimming at speeds above the minimum cruising speed. Indirect evidence from a number of teleost species (e.g., Greer Walker and Pull 1973) indicated that the white fibres are active at these intermediate swimming speeds, as did the direct electromyographic investigations of Hudson (1973). More recently, several workers have suggested that fibres of intermediate type are recruited as swimming speed rises from the minimal cruising speed, before white fibres are activated and the fish attains its maximal sustained speed. In this note, we report electromyographic observations on various teleosts swimming at controlled speeds in a tunnel respirometer, which show that the activity of the myotomal fibre types during sustained swimming is different in different fishes.

Material and Methods

We studied herring, carp, and trout. Juvenile Pacific herring, *Clupea harengus pallasi* Valenciennes, 15-17.5 cm FL (fork length) were caught by seining in the Georgia Straits, B.C., and held in circulating seawater at the Department of Zoology, University of British Columbia, until swum in a tunnel respirometer (Brett 1964). Herring are delicate fish and did not settle quietly in the respirometer at flow lengths below 2-3 body lengths per second (BL/s). Instead, they darted upstream and fell back again in an irregular manner, so that it was necessary to force them to swim at such speeds from their first entry to the apparatus, without the acclimation period usual when working with other fishes.

Varnished copper wire (40 standard wire gauge) electrodes bared at the tips were placed in the postanal myotomes. The fish were anaesthetized with MS-222[1] (Sandoz) and the electrodes sutured to the dorsal surface before being led downward and backward to enter the myotomes. After recovery for 30 min or so in a bucket of seawater, the fish were introduced to the respirometer and muscle potentials recorded on a Gould Brush 220 pen recorder via Tektronix 122 preamplifiers. It proved difficult to record from electrodes whose tips lay amongst the white muscle fibres, but activity from

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

these fibres was picked up by electrodes whose tips lay in the thin lateral red muscle strip. Relative proportions of red and white muscle fibres were determined by dissection, and their innervation patterns were examined in Formalin-fixed material. Cryostat sections stained for lipid and for succinic dehydrogenase by routine methods were used to distinguish different fibre types.

Similar studies were carried out on carp, *Cyprinus carpio* Linnaeus, 25-30 cm FL, caught by seining in the Fraser Valley, B.C., and rainbow trout, *Salmo gairdneri* Richardson, 17-30 cm FL obtained from a commercial supplier. Before trial in the respirometer both species were held in circular tanks around which water was pumped to give a constant flow of 30-40 cm/s around the circumference where the fish normally swam. For these freshwater fish, much improved signal : noise ratios were obtained by adding small amounts of seawater to the freshwater in the respirometer; this did not affect the behavior of the fish, which were allowed to acclimate for 18-20 h in the apparatus before testing.

Results

Pacific Herring

The records of muscle activity shown in Figure 1A-C are from electrodes with their tips lying in the lateral strip of red muscle. These records show that bursts of irregular potentials around 200-300 μV peak to peak are recorded from the red fibres during slow sustained swiming, becoming more synchronous and shorter as swimming speed increases and tail beat frequency rises. At sustained

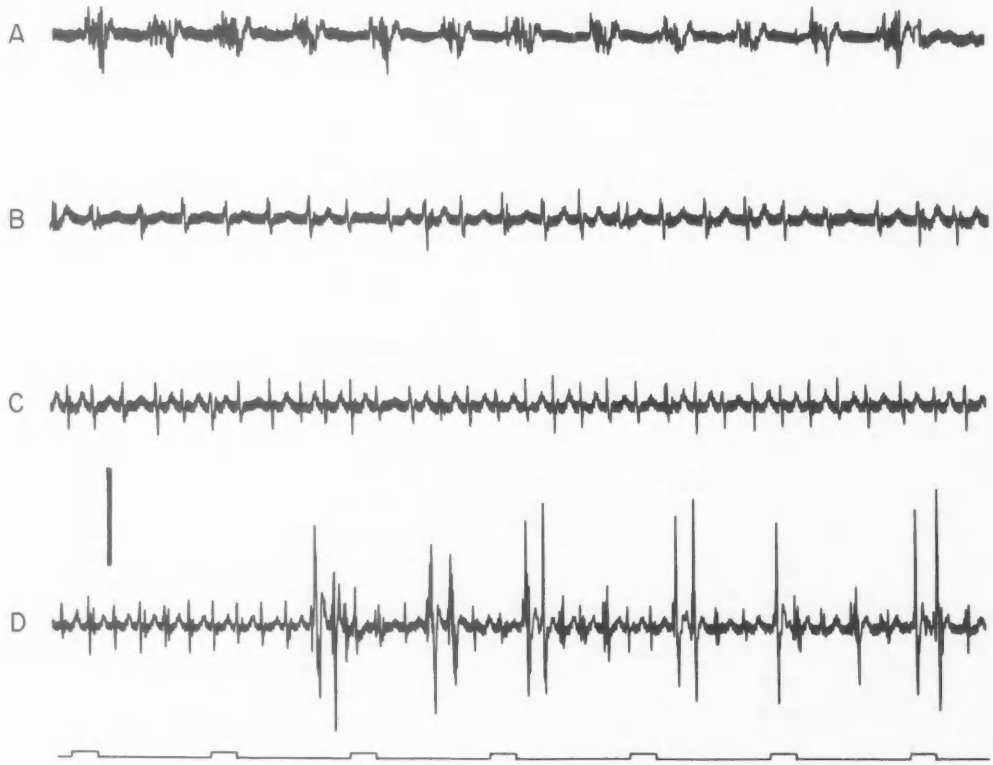

FIGURE 1.—Records from lateral red muscle of a juvenile Pacific herring (16.4 cm fork length) swimming at different speeds. A: 1.8 body lengths per second; B: 2.8 body lengths per second; C: 3.1 body lengths per second; and D: 4.3 body lengths per second. Note gradually increasing synchrony of potentials as swimming speed and tail beat frequency rise (A-C), and the appearance of large potentials in D (picked up from underlying white fibres) when the fish struggled to maintain position at high flow speed. Vertical bar: 500 μV; time marker: seconds.

swimming speeds up to 4-5 BL/s, these are the only kind of potentials recorded; no larger potentials are observed. Because herring are delicate fish, velocity/endurance experiments in respirometers or water tunnels are likely to underestimate their real capabilities, for it is probable that they slowly deteriorate during their sojourn under experimental conditions. Our limited series of measurements of sustained swimming speeds (Figure 2) showed that juvenile herring were able to maintain speeds around 4 BL/s for periods of at least 5 h, a performance about double that previously observed by Boyar (1961), but similar to that seen in large circular tanks by Hempel (in Blaxter 1969).

Boyar's study was very much more extensive than ours; some of his results are plotted in Figure 2 for comparison, where it can be seen that the form of the velocity/endurance curves we obtained is similar to those found for other fish (e.g., Hunter 1971). It seems probable that 4-5 BL/s represents a sensible upper value for continuous sustained cruising by herring of this size.

If the speed of flow in the respirometer is increased above this speed, or if the fish becomes progressively exhausted, it intersperses periods of steady swimming, as before, (during which it slowly falls back to the downstream electrified grid) with a few rapid tail beats, which drive it upstream, and the cycle is repeated. During these rapid beats (Figure 1D), large potentials around 1 mV are observed. Similar potentials are seen when the fish is struggling, and there can be no doubt that (as in dogfish, Bone 1966) the electrodes in the red fibre layer pick up these large potentials from the underlying white fibres. White fibres in herring are similar to those of dogfish in that they are focally innervated (Bone 1964) and they must therefore propagate action potentials. The white fibre system in herring was rapidly exhausted, for the fish could not swim at velocities above 5 BL/s for more than 1-2 min (as indicated in Figure 2). Thus there is good accord between our electromyographic observations and the values obtained for maximum sustained swimming velocities: in herring only red muscle fibres are employed during sustained cruising.

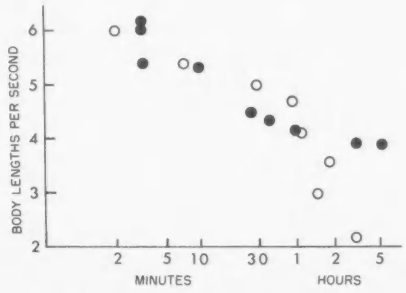

FIGURE 2.—Swimming speeds (in body lengths per second) plotted against the time that the speeds were sustainable (abscissa). Dots: present observations; open circles: data plotted for comparable fish from Boyar (1961). Note the different forms of the velocity/endurance curves given by the two sets of fish, probably the consequence of damage to Boyar's fish in his apparatus.

Histologically, the red and white fibres are different from each other. The red fibres are of more or less uniform diameter, are multiply innervated, and lipid and succinic dehydrogenase (SDH) positive. In contrast, the white zone of the myotome contains both large fibres, and much smaller fibres arrayed around them in a sort of lattice. Both types contain little lipid, are SDH negative, and there are no intermediate fibres either in the juvenile herring which we examined in the respirometer, or in adults. These histological arrangements are summarized in Figure 3A.

Carp

The carp used were much more robust and larger fish than the Pacific herring and it proved possible to make simultaneous recordings of activity within white and red portions of the myotomes. The results obtained were entirely different from those seen in the herring. At speeds between 0.5 BL/s (the lowest speed at which the fish would swim reliably) and the maximum speed used, around 4 BL/s, electrical activity was always detectable from both sets of electrodes in red and white zones of the myotomes (Figure 4). As speed increases from the lowest values, the bursts of activity from each zone became more synchronous and shorter and their amplitude increased. Occasional spikes of greater amplitude were observed from the white muscle zone (Figure 4B), these were faster events than those composing the remainder of the motor bursts. When the fish was swimming near the maximum speed sustainable in the respirometer (Figure 4C), these rapid potentials formed the larger part of the motor bursts and were always seen on both red and white recordings, though smaller from the former. Presumably, they represent spikelike activity from the white zone of the myotome, picked up (as in herring) by electrodes in the red zone. Since the red and white electrodes did not lie in the same

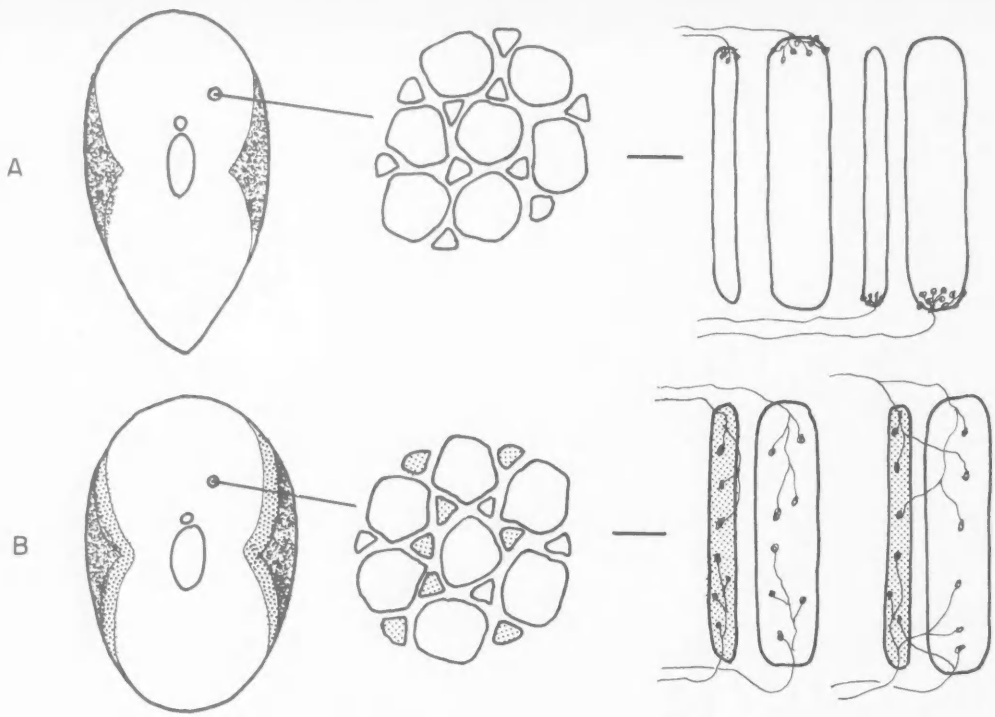

FIGURE 3.—Diagram summarizing the organization of white muscle fibres in the myotome of Pacific herring (A), compared with those of rainbow trout and carp (B). It is not known whether a single axon may supply both large and small white fibres in herring (though both are focally innervated), nor is it known which of the two alternative innervation patterns for rainbow trout and carp are actually present. An overlap of innervation between small and large fibres seems most likely. Note the presence of intermediate fibres between red and white zones of the myotome in carp and rainbow trout; they are absent in herring. (B partly after Patterson et al. 1975 and Johnston et al. 1977.)

myotome (though on the same side of the fish and fairly close to each other), the appearance of occasional spikelike potentials in the white zone was not always reflected directly in the record from the red. At lower swimming speeds, when the electrodes in the white zone did not pick up spikelike potentials at every tail beat, higher recording speed (Figure 4D) showed the variety of response from the white zone of the same myotome at successive tail beats.

Spikelike potentials were present (although usually <0.5 mV in amplitude) and were often reflected at lesser amplitude by the electrodes in the red portion of the myotome, but there were also much smaller irregular potentials from the white region of the myotome, resembling the smaller irregular potential bursts from the multiply innervated red fibres. In carp, both red and white muscle fibres are multiply innervated and there are intermediate fibres lying between red and white fibre zones (Figure 3B). The electrodes in the white portion of the myotome were placed close to the spinal column so that they did not lie near the intermediate zone recently described by Johnston et al. (1977).

Our results clearly indicated that the white fibres were active even at low swimming speeds, and that the activity at these speeds did not resemble the spikelike muscle potentials observed when the fish are swimming faster.

Rainbow Trout

Rainbow trout were examined last of the three fish studied and, to our surprise, gave results comparable with those from the herring, although in salmonids the white fibres are multiply innervated, as they are in carp. At speeds below 2 BL/s, no activity was detectable from the white (mosaic)

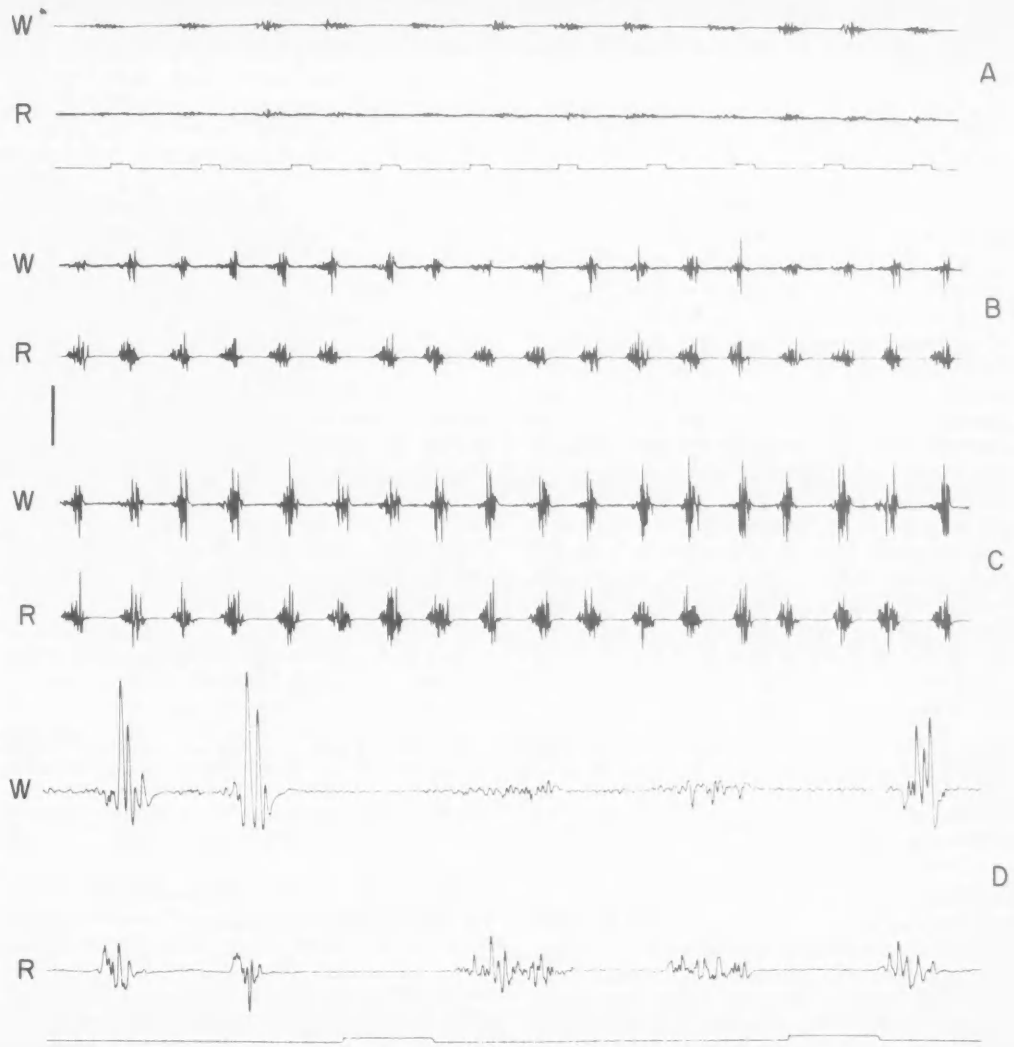

FIGURE 4.—Records of activity from red (R) and white (W) regions of a carp myotome at different swimming speeds. A: 0.75 body length per second; B: 0.9 body length per second; C: 1.26 body lengths per second: and D: 2.0 body lengths per second. Note that the white fibres are active even at low swimming speed and that there is spikelike activity at each tail beat in C. The lowest record (D) taken at higher chart speed shows the appearance of irregular bursts containing spikelike potentials. Note pick-up of these events by the overlying red fibre electrode. Vertical bar: 500 μV; time marker: seconds.

zone of the myotome: 1-200 μV potentials of the usual kind were obtained from the lateral red musculature (Figure 5A). When startled, a few rapid tail beats drove the fish forward and, under these conditions, larger spikelike potentials around 0.5 mV peak to peak were recorded from the white zone of the myotome corresponding to the rapid tail beats. As can be seen from Figure 5B, these events were picked up at lower amplitude by the electrodes whose tips lay in the lateral red muscle layer. After a few rapid tail beats, the fish coasted forward before dropping back and resuming regular swimming: the normal rhythm of the red fibre system was inhibited for a few cycles.

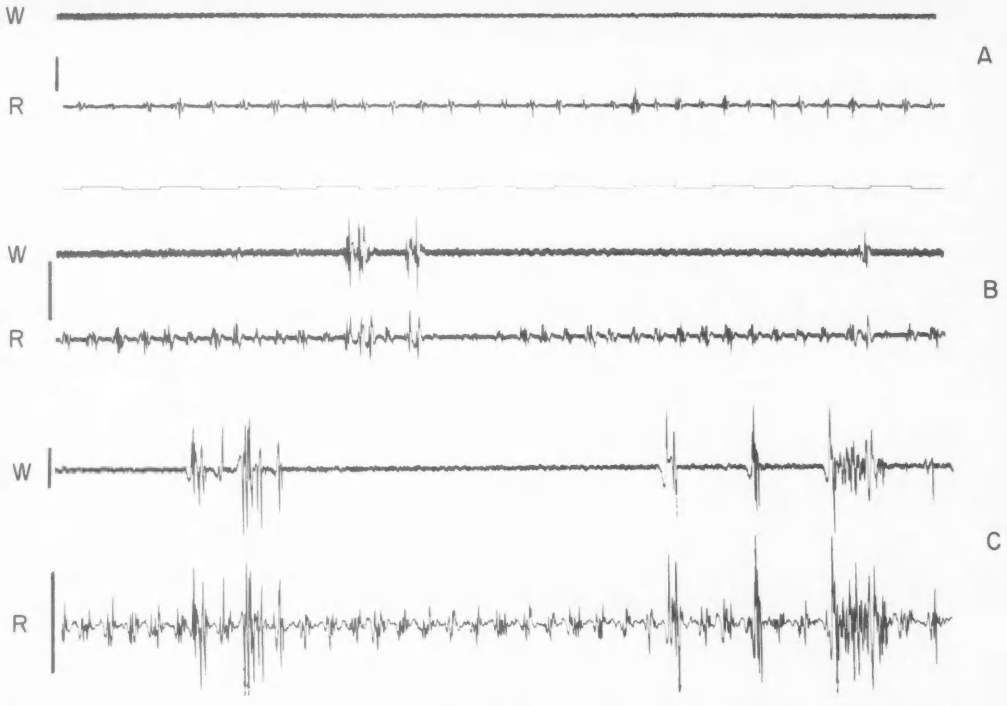

FIGURE 5.—Records of activity from red (R) and white (W) regions of the myotome of different rainbow trout swimming at various speeds. A: 1.8 body lengths per second; B: 4.6 body lengths per second; C: 2.2 body lengths per second. Note that during regular sustained swimming involving red muscle activity, no activity is detected from the white zone of the myotome. Occasional spikelike activity from the white zone of the myotome is seen in B and C (also picked up by the electrode lying in the overlying red zone of the myotome), sometimes inhibits the red muscle bursts (B) and sometimes does not (C). Vertical bars: 1 mV; time marker: seconds.

A single rapid tail beat (to the right of the record) interrupted the red muscle for a single cycle. At higher sustained speeds, above 2 BL/s (as in Figure 5C) this inhibition of red activity following single rapid movement no longer took place. Rather, the behavior was similar to that of the herring in that the fish fell gradually back despite the regular activity of the red system, until driven forward again by a few rapid beats; to drop back again and repeat the cycle until the white system was exhausted. Under these conditions, the fish did not "coast" following rapid tail movements.

No electrical activity was observed from the white zone of the myotome (the so-called mosaic zone) apart from the spikelike potentials shown in Figure 5B and C, although particular pains were taken to ensure that the electrodes were recording satisfactorily. All the fish recorded from gave this same result. We conclude from our observations that this part of the motor system is not active at speeds below 2-2.5 BL/s. Figure 3B summarizes the structure of the system.

Discussion

Our observations have shown once again that the lateral red musculature is used by fish for sustained slow cruising, and that rapid movements of the tail are brought about by the activity of the white motor system, during which spikelike potentials can be recorded from the white zone of the myotome. At intermediate speeds, there are manifest differences between different fishes.

The simplest situation is shown by the Pacific herring, where sustained activity depends only on the activity of the red motor system of the myotome: the white fibres play no part in any activity except rapid movements of short duration. It is true that such movements can "top up," as it were, the sustained activity of the red motor sys-

tem, but this process cannot be long continued: in the respirometer flow velocities which overload the red system and involve occasional activity from the white system soon exhaust the fish. Presumably this artificial situation, where the fish are forced to swim at such speeds, is not found in nature.

The taxonomic position of clupeids is not yet agreed upon (see Greenwood et al. 1966), but in the organization of their myotomal motor system they show the primitive pattern of focal innervation of the white fibres (Bone 1970) found also in elasmobranches, Agnatha, and dipnoi, but in few other teleosts.

We may surmise that in all fish where the white motor system is innervated in this way, sustained swimming will be the responsibility of the red system alone, as it is in herring and dogfish. It is important to notice that this is not to say that gradation may not take place separately within either system. For example, there are five fibre types in the dogfish myotome (three slow and two fast) distinguishable by histochemical and ultrastructural criteria, and it is entirely reasonable to suppose that the two fast fibre types are recruited for movements of different rapidity as Kryvi and Totland (1977) have suggested. At present, our preliminary ultrastructural and histochemical investigations of young and adult herring myotomal fibres have only shown one type of red fibre and two types of white fibre. The two white fibre types may operate at different stages during rapid swimming, but there is no direct evidence for this assumption, and it may be more reasonable to interpret the smaller white fibres as growth stages in the development of the larger (see Bone in press).

In carp, the situation during sustained swimming at all speeds is entirely different. There is inevitably some ambiguity in the interpretation of electromyographic records since the position of the electrode tip may not be certainly known, and the records obtained may be from nearby small electrical events or from distant larger ones, but it certainly does not seem probable that the small events recorded from the carp white muscle at slow sustained swimming speeds can have been picked up from the distant red muscle system. To judge from our records taken deep within the white muscle, as far as possible from the lateral red strip, some fibres within the white zone are active even at the slowest sustained speeds, and this activity increases as the fish increases its swimming speed. This kind of electrical activity at the slower sustained speeds is very similar to that of the red motor system, and presumably represents the activity of fibres which are not propagating muscle action potentials. Such records could not, naturally, be obtained from the white system of fish where the white fibres are focally innervated, and in fact are not seen in herring or dogfish. At higher sustained speeds, or when the carp is disturbed, much larger rapid potentials are observed from the electrode within the white zone. Plainly, two alternative explanations are possible for the variety of electrical response from a single recording site within the white muscle. Either the electrode tip lies close to fibres of two different types, one of which is capable of propagating muscle spikes and the other is not. In this situation, the potentials observed simply reflect the fact that the former system is only activated at higher speeds, the latter operating during slow swimming and so resembling the red motor system. In other words, in the carp myotome, the arrangement is essentially a mosaic one, in which red fibres are intermingled with the usual fast fibres of the white zone. Or, alternatively, the white zone contains only a single muscle fibre type, which is capable of local contractions not involving muscle action potentials, but can also be stimulated to twitch rapidly and, in this state, propagates muscle action potentials. As pointed out earlier (Bone 1975) this would be an ingenious way of ensuring for a single muscle fibre that it always operated at the flattened upper part of the power curve, contracting at very different rates whilst swimming slowly and rapidly.

Our electromyographic records do not allow us to distinguish between these two alternatives but there is no evidence from the histochemical studies by Patterson et al. (1975), or the recent excellent paper by Johnston (1977), that there are "red" fibres in the white zone of the carp myotome. These authors have demonstrated clearly, however, that there is a zone of intermediate fibres between the lateral red and deep white fibres of the carp myotome. They have also shown that these three fibre types are active at different swimming speeds. At 1 BL/s only red fibres were found to be active; at 1.3-1.5 BL/s both red and pink fibres were active, whereas at 2.0 BL/s and above, electrical activity appeared from the white zone of the myotome. These results clearly indicated the sort of recruitment of intermediate fibres at intermediate sustained swimming speeds

which was implied by their accompanying biochemical studies. Interestingly enough, Johnston et al. (1977) observed the same kind of electrical activity from the white zone of the myotome that we observed at low speeds, and it seems therefore extremely probable that such activity (around 75 μV in their records at 2.0 BL/s) is indeed generated by muscle fibres in the white zone. They did not observe spikelike activity from the white zone, presumably because their fish were not swimming sufficiently fast, i.e., they investigated only the lower sustained swimming speed range.

It is then still an open question whether individual fibres in the white zone can sometimes operate producing only local potentials, at other times generating muscle action potentials; or whether there are two different fibre types in the white zone, as yet not distinguishable histochemically. We incline to the former opinion, but to settle the matter evidence from intracellular studies will be essential.

In rainbow trout, our results were again different. We obtained no evidence for activity of the mosaic zone of the myotome during sustained activity even at 4.5 BL/s (the maximum speed at which we could swim the smaller fish). Considering Hudson's (1973) electromyographic evidence from the same species, where he observed activity from the mosaic zone at speeds above 3.0BL/s, this seemed at first rather surprising.

However, the fish Hudson used came from a stock of notoriously poor swimming performance (see Webb 1971), and it is therefore quite possible that we never attained the critical speed at which the mosaic muscle became active in our fish. The main muscle mass in rainbow trout consists of a mosaic of small reddish fibres scattered amongst larger pale fibres (Johnston et al. (1975) have studied them histochemically), and it is thus unclear whether the low-level electrical activity which Hudson (1973) recorded from this region (similar to that which we found in carp white muscle) comes from the same fibres as those generating muscle action potentials during burst swimming. In other words, the two kinds of electrical responses from the rainbow trout mosaic muscle may result from the activity of two different kinds of muscle fibres.

Fish are so diverse, and their patterns of life so varied, that it is hardly surprising that there should be differences on their locomotor musculature. We perhaps ought rather to be surprised at the general uniformity of design of the locomotor system imposed by the aquatic medium. It seems probable, from the distribution of patterns of innervation amongst different fish groups, and indeed amongst the teleosts alone, that focally innervated, twitch fibres operating by anaerobic glycolysis for short bursts of swimming represent the primitive arrangement of the aquatic fast motor system (see Bone 1970).

This fast-motor system contrasts markedly with the universally found multiply innervated nontwitch red fibre system for sustained movement that operates aerobically. However, histological and biochemical investigations of the white myotomal zones of some specialized teleosts such as tuna (Guppy et al. in press) or carp (Johnston et al. 1977) have shown a definite aerobic capacity in the white fibre system, and the original simple dichotomy between anaerobic white fibres and aerobic red fibres rather naively suggested from elasmobranch studies (Bone 1966) is plainly not a good description of the operation of the myotome in all teleosts.

On the whole, it seems reasonable to assume that in most teleosts where the white portion of the myotome is multiply innervated, there will be aerobic intermediate fibres for use during fast sustained cruising, and that at the maximum cruising speed at least some fibres in the white zone of the myotome will also be active aerobically. This seems to be the situation in rainbow trout, and it probably also obtains in most scombrids.

The situation in carp is less clear. The work of Smit et al. (1971) has shown that goldfish (close to carp) are able to sustain high speeds in a respirometer apparently using the white muscle system anaerobically. In line with this, Driedzic and Hochachka (1975) were unable to detect other energy sources than anaerobic glycolysis in carp white muscle, and Johnston et al. (1977) only found low values of aerobic enzymes in this system. We have provided clear evidence that the white motor system is operating over a wide speed range, from the lowest speed at which the fish will swim in the respirometer, and it seems bizarre that a relatively inefficient anaerobic metabolism should drive sustained activity. At low sustained swimming speeds carp might keep in overall aerobic balance by transferring lactate from the white zone to other regions of the body, where lactate could be completely metabolized (Bone 1975). Driedzic and Hochachka found only low lactate levels in the white zone after severe

hypoxic stress, and suggested that this could be explained by lactate transfer out of the system. It is very hard to believe that such a process could account for the extremely interesting results of Smit and his colleagues (Driedzic and Hochachka entitled their paper "The unanswered question of high anaerobic capabilities of carp white muscle"), and we agree with Johnston et al. (1977) in their conclusion that carp would appear to be an ideal species for studying the relationship between muscle design and locomotor function.

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SUMMER FOOD OF THE PACIFIC COD, *GADUS MACROCEPHALUS*, NEAR KODIAK ISLAND, ALASKA[1,2,3]

The Pacific cod, *Gadus macrocephalus* Tilesius, was the target of the earliest United States commercial fishery in the North Pacific (Buck[4]). Its fleet, organized in spring 1865 (Bean 1887), began to fish along the Alaska Peninsula and the Aleutian Islands and eventually expanded into the Bering Sea (Cobb 1916). Dwindling stocks and poor market prices ultimately resulted in the collapse of this fishery shortly after World War II (Ketchen 1961).

Growing pressures in recent years on domestic fishing stocks, in addition to increased worldwide protein demand, improved technological skills and readily available investment capital, have resulted in renewed interest in Pacific cod in the United States (Jones 1977). A bottomfish survey off the coast of Kodiak Island and throughout Shelikof Strait by the National Marine Fisheries Service in 1973 showed the Pacific cod to be one of the most abundant fishes inhabiting the area and the standing stock was conservatively estimated to be about 36,363 t (Hughes and Parks 1975). A small experimental trawl fishery for the Pacific cod and other bottom fishes has been proposed for the Kodiak region by Jones (1977).

Preliminary examination of *G. macrocephalus* stomach contents by Alaska Department of Fish and Game (ADF&G) biologist Guy C. Powell and the author during ADF&G crab investigations off Kodiak Island indicated a high frequency of occurrence of the commercially important snow crab, *Chionoecetes bairdi*. In view of the probable predation pressure on existing snow crab populations by *G. macrocephalus* and in view of the potential commercial importance of the Pacific cod, the summer food habits of this fish in the Kodiak area were examined by me. Ancillary goals included a comparison of food data from pot- and trawl-captured cod.

Methods

Specimens were taken near Kodiak Island, Alaska, (Figure 1) in conjunction with the crab-assessment studies of ADF&G and the surveys of the International Pacific Halibut Commission. Fishing gear consisted of commercial king crab pots, measuring 203 × 203 × 76 cm (inside) and weighing 340 kg; baited with chopped, frozen herring. Webbing was #72 tarred nylon thread with mesh stretched to 7.6 cm. The gear used on the halibut-survey vessels in July 1975 and July 1976 was a standard 400-mesh Eastern otter trawl (Greenwood 1958). Sampling by pots was from 26 June to 3 August 1973, 28 June to 31 July 1974, and 30 June to 27 July 1975. Stations usually consisted of 4-12 pots in a straight line, equally spaced every 0.46 km. Gear was pulled every 18-24 h except when weather conditions prolonged fishing time.

A haphazard sample of 3,933 of Pacific cod was taken from 10,857 cod caught in pots (the number sampled was contingent on the shipboard time available for analysis of stomach contents). Food items were identified to the lowest taxon practical aboard ship, and unidentifiable contents were preserved for later laboratory examination. Analysis of stomach contents was carried out using the frequency of occurrence method in which the prey organisms are expressed as the percent of stomachs containing various food items from the total number of stomachs analyzed. Cod were arbitrarily divided into 33-52 cm, 53-72 cm, and 73-92 cm size (total length) groups for analysis.

The frequency of occurrence method was also used for food data from trawl-caught Pacific cod. The stomachs of 344 cod were examined from 24 trawl stations, which were located in the same general area as the pot stations (Figure 1).

Results and Discussion

As determined from the pot data, the summer diet of *G. macrocephalus* was fishes, crabs, shrimps, and amphipods, in decreasing order of occurrence (Table 1). The most frequently occurring fish was walleye pollock, *Theragra chalcogramma*. Flatfishes (Pleuronectidae) and Pacific sand lance, *Ammodytes hexapterus*, were also frequent. Suyehiro (1942:233-236), Moiseev (1953, 1960), and Mito (1974) also reported that Pacific cod feed on these fishes.

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[3]Based on a thesis submitted in partial fulfillment of the requirements for the M.S. degree, University of Alaska.

[4]Buck, E. H. 1973. Alaska and the law of the sea. National patterns and trends of fishery development on the North Pacific. Alaska Sea Grant Rep. No. 73-4, 65 p.

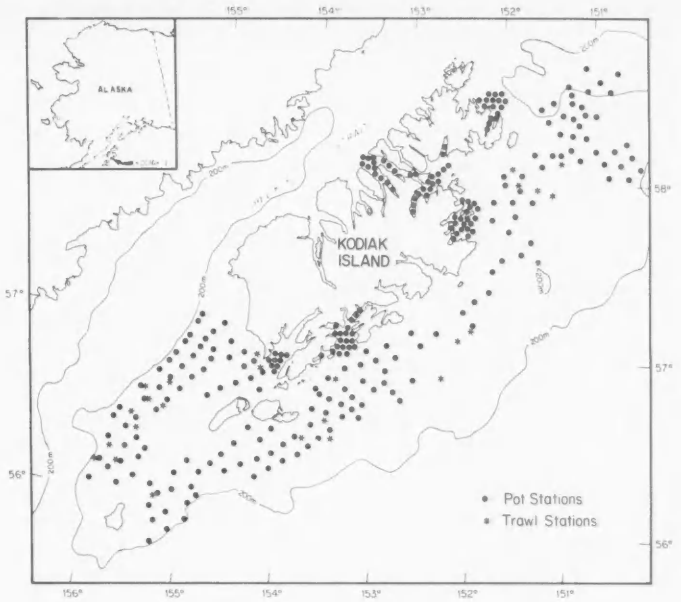

FIGURE 1.—Stations near Kodiak Island, Alaska, where Pacific cod were collected by pots and trawls during summers of 1973-75.

Crab occurrences were dominated by juvenile *C. bairdi*. Snow crabs were the single most frequently occurring food species found in Pacific cod stomachs and occurred in nearly 40% of the cod (Table 2). The average number of snow crabs occurring in cod feeding on snow crabs was 3.3 and they ranged from 1.8 to 70 mm carapace width[5] (Hilsinger et al.[6]); 78% were between 7 and 23 mm. Up to 32 crabs were found in a single cod stomach.

Chionoecetes bairdi had become important in the Alaskan and world markets with landings for Kodiak increasing from 50.3 t in 1967 to 12,400 t in 1976 (North Pacific Fishery Management Council[7]). Since juvenile snow crabs are a major item in the diet of the Pacific cod, reduction of cod stocks by the anticipated new bottomfish fishery should improve the chances for survival of young crabs. Enhanced recruitment of snow crabs to fishable stocks might result from such improved survival.

Pandalid and crangonid shrimps were important in the diet of the Pacific cod in the Kodiak area, a region where both groups are abundant in species and numbers (Ronholt 1963; Barr 1970; Feder and Jewett[8]).

Anonyx nugax may be the principal amphipod. Amphipods which were occasionally preserved from the stomach contents as well as from the perforated bait cans in the crab pots were later identified as *A. nugax*. Because of attraction to the bait, the occurrence of amphipods in stomachs of the pot-caught cod was probably artificially high.

Occurrence of food organisms in trawl-caught cod, in decreasing order was also fishes, crabs, shrimps, and amphipods (Table 3). The most common fishes were *A. hexapterus*, *T. chalcogramma*, and flatfishes. The most frequently consumed crab was *C. bairdi*. Shrimps were primarily Crangonidae.

Wilcoxon's paired-sample test indicated no significant difference ($\alpha = 0.05$) among food groups from cod caught by the two methods, or between sexes (Table 4). No sex differences were found in

[5]Females mature at about 72 mm carapace width (Hilsinger et al. see footnote 6) and males at about 110 mm carapace width (Brown and Powell 1972).

[6]Hilsinger, J. R., W. E. Donaldson, and R. T. Cooney. 1975. The Alaska snow crab, *Chionoecetes bairdi*, size and growth. Unpubl. manuscr., 38 p. Univ. Alaska Sea Grant Rep. No. 75-12 (Inst. Mar. Sci. Rep. No. 75-6).

[7]Fishery Management Plan and environmental impact statement for the tanner crab off Alaska. Sept. 23, 1977. Unpubl. manuscr., 346 p., prepared by the North Pac. Fish. Manage. Counc.

[8]Feder, H. M., and S. C. Jewett. 1977. The distribution, abundance, and diversity of the epifauna of two bays (Alitak and Ugak) of Kodiak Island, Alaska. Inst. Mar. Sci. [Univ. Alaska] Rep. R77-3, 74 p.

TABLE 1.—Frequency and percent frequency of occurrence of summer food items in stomachs of *Gadus macrocephalus* collected during 1973-75 by pots near Kodiak Island, Alaska. N = number of stomachs examined. Subtotals in parentheses.

FOOD ITEMS	1973 N=689 Freq.	1973 % Freq.		1974 N=1183 Freq.	1974 % Freq.		1975 N=2061 Freq.	1975 % Freq.		TOTAL 1973-75 N=3933 Freq.	TOTAL 1973-75 % Freq.	
Coelenterata												
Hydrozoa (hydroids)	2	0.3		-	-		1	0.1		3	0.08	
Scyphozoa (jellyfishes)	-	-		-	-		1	0.1		1	0.03	
Anthozoa (anemones)	5	0.7	(1.0)	3	0.3		1	0.1	(0.3)	9	0.2	(0.31)
Annelida												
Polychaeta (segmented worms)	-	-		53	4.5		74	3.6		127	3.2	
Aphrodita sp.	15	2.1		10	0.9	(5.4)	24	1.2	(4.8)	49	1.2	(4.4)
Mollusca												
Polyplacophora (chitons)	-	-		1	0.1		-	-		1	0.03	
Pelecypoda (clams, mussels, cockles)												
Astarte polaris	-	-		1	0.1		1	0.1		2	0.05	
Chlamys sp.	-	-		-	-		1	0.1		1	0.03	
Clinocardium sp.	1	0.1		-	-		4	0.2		5	0.1	
Cyclocardia crassidens	1	0.1		1	0.1		1	0.1		3	0.08	
Cyclocardia crebricostata	1	-		1	0.1		-	-		1	0.03	
Cyclocardia sp.	-	-		-	-		2	0.1		2	0.05	
Glycymeris subobsoleta	1	0.1		-	-		-	-		1	0.03	
Hiatella arctica	1	0.1		-	-		-	-		1	0.03	
Limopsis akutanica	-	-		1	0.1		-	-		1	0.03	
Limopsis vaginatus	-	-		2	0.2		-	-		2	0.05	
Macoma brota	-	-		-	-		1	0.1		1	0.03	
Macoma calcarea	-	-		-	-		1	0.1		1	0.03	
Macoma expansa	1	0.1		-	-		-	-		1	0.03	
Macoma moesta	-	-		1	0.1		1	0.1		2	0.05	
Macoma sp.	1	0.1		1	0.1		1	0.1		3	0.08	
Modiolus sp.	-	-		-	-		2	0.1		2	0.05	
Musculus discors	-	-		-	-		1	0.1		1	0.03	
Musculus olivaceus	1	0.1		1	0.1		1	0.1		3	0.08	
Nucula tenuis	1	0.1		-	-		4	0.2		5	0.1	
Nuculana fossa	30	4.3		43	3.6		36	1.8		109	2.7	
Panomya ampla	1	0.1		-	-		-	-		1	0.03	
Patinopecten caurinus	-	-		7	0.6		5	0.2		12	0.3	
Pododesmus macroschisma	-	-		1	0.1		1	0.1		2	0.05	
Psephidia lordi	1	0.1		-	-		-	-		1	0.03	
Punctureila galeata	-	-		1	0.1		-	-		1	0.03	
Serripes groenlandicus	-	-		3	0.3		3	0.1		6	0.1	
Siliqua sloati	-	-		-	-		1	0.1		1	0.03	
Tellina nuculoides	-	-		-	-		1	0.1		1	0.03	
Velutina velutina	1	0.1		-	-		-	-		1	0.03	
Yoldia beringiana	2	0.3		-	-		5	0.2		7	0.2	
Yoldia myalis	-	-		2	0.2		-	-		2	0.05	
Yoldia thraciaeformis	-	-		1	0.1		-	-		1	0.03	
Yoldia sp.	7	1.0		4	0.3		-	-		11	0.3	
Unidentified Pelecypods	26	3.8		27	2.3		53	2.6		106	2.7	
Gastropoda (snails)												
Admete couthouyi	-	-		-	-		1	0.1		1	0.03	
Aforia circinata	-	-		-	-		1	0.1		1	0.03	
Amphissa columbiana	1	0.1		-	-		1	0.1		2	0.05	
Beringius kennicotti	-	-		-	-		1	0.1		1	0.03	
Boreotrophon pacifica	-	-		1	0.1		1	0.1		2	0.05	
Buccinum sp.	1	0.1		-	-		-	-		1	0.01	
Colus halli	-	-		-	-		2	0.1		2	0.05	
Cylichna alba	1	0.1		1	0.1		-	-		2	0.05	
Fusitriton oregonensis	1	0.1		-	-		2	0.1		3	0.08	
Margarites baxter	-	-		1	0.1		-	-		1	0.03	
Margarites obscura	-	-		1	0.1		2	0.1		3	0.08	
Margarites pupillus	-	-		-	-		1	0.1		1	0.03	
Mitrella gouldi	-	-		-	-		1	0.1		1	0.03	
Natica aleutica	1	0.1		2	0.2		-	-		3	0.08	
Natica clausa	-	-		1	0.1		-	-		1	0.03	
Natica sp.	-	-		-	-		5	0.2		5	0.1	
Neptunea sp.	1	0.1		-	-		1	0.1		2	0.05	
Polinices [illegible]	-	-		-	-		1	0.1		1	0.03	
Polinices pallida	2	0.3		2	0.2		3	0.2		7	0.2	
Solariella varicosa	-	-		1	0.1		-	-		1	0.03	
Tachyrhynchus sp.	-	-		1	0.1		-	-		1	0.03	
Trichotropis cancellata	1	0.1		1	0.1		3	0.2		5	0.01	
Turridae	-	-		-	-		1	0.1		1	0.03	
Unidentified gastropods	1	0.1	(11.6)	26	2.2	(11.9)	34	1.7	(10.3)	61	1.5	(10.2)
Cephalopoda												
Octopi	53	7.6		108	9.1		164	8.0		326	8.3	
Squid	-	-		1	0.1	(9.2)	-	-		-	-	
Arthropoda												
Crustacea												

TABLE 1.—Continued.

FOOD ITEMS	1973 N=689 Freq.	1973 % Freq.		1974 N=1183 Freq.	1974 % Freq.		1975 N=2061 Freq.	1975 % Freq.		TOTAL 1973-75 N=3933 Freq.	TOTAL 1973-75 % Freq.	
Malacostraca												
Euphausiacea (krill) and Mysidacea (mysids)	20	2.9		34	2.9		181	8.8		235	6.0	
Isopoda (pill bugs)	3	0.4		4	0.3		10	0.5		17	0.4	
Amphipoda (sand fleas)	192	27.8		195	16.5		407	19.8		794	20.2	
Ampelisca macrocephala	–	–		–	–		52	2.5	(22.3)	52	1.3	(21.5)
Decapoda												
Pandalidae (shrimps)	67	9.7		118	10.0		–	–		185	4.7	
Pandalus borealis	–	–		–	–		166	8.1		166	4.2	
Pandalopsis dispar	–	–		4	0.3		19	0.9		23	0.6	
Pandalus goniurus	–	–		–	–		4	0.2		4	0.1	
Pandalus hypsinotus	–	–		–	–		7	0.3		7	0.2	
Pandalus montagui tridens	–	–		–	–		8	0.4		8	0.2	
Pandalus platyceros	–	–		1	0.1		3	0.2		4	0.1	
Crangonidae (shrimps)	77	11.1		95	8.0		286	13.9		458	11.6	
Argis crassa	–	–		–	–		3	0.2		3	0.08	
Sclerocrangon boreas	–	–		–	–		5	0.2		5	0.1	
Hippolytidae												
Spirontocaris sp.	–	–		–	–		5	0.2		5	0.1	
Unidentified shrimps	131	19.0	(39.8)	82	6.9	(25.3)	171	8.3	(32.9)	384	9.8	(31.8)
Paguridae (hermit crabs)	24	3.4		21	1.8		55	2.7		100	2.5	
Elassochirus cavimanus	–	–		–	–		2	0.1		2	0.05	
Elassochirus tenuimanus	–	–		1	0.1		3	0.2		4	0.1	
Lithodidae (crabs)												
Paralithodes camtschatica	2	0.3		9	0.8		31	1.5		42	1.1	
Placetron wosnessenskii	–	–		1	0.1		2	0.1		3	0.08	
Rhinolithodes wosnessenskii	–	–		–	–		1	0.1		1	0.03	
Galatheidae (crabs)												
Munida quadrispina	–	–		–	–		1	0.1		1	0.03	
Cancridae (crabs)	–	–		1	0.1		13	0.6		14	0.4	
Cancer sp.	4	0.5		–	–		–	–		4	0.1	
Telmessus cheiragonus	1	0.1		–	–		2	0.1		3	0.08	
Pinnotheridae (pea crabs)												
Pinnixa sp.	5	0.7		36	3.0		23	1.1		64	1.6	
Majidae (spider crabs)												
Chionoecetes bairdi	281	40.7		428	36.2		735	35.6		1444	36.7	
Hyas lyratus	13	1.8		44	3.7		42	2.0		99	2.5	
Oregonia gracilis	–	–		3	0.3		6	0.3		9	0.2	
Unidentified crabs	12	1.7	(49.2)	3	0.3	(46.4)	4	0.2	(44.7)	19	0.5	(46.0)
Echinodermata												
Asteroidea (sea stars)	1	0.1		2	0.2		1	0.1		4	0.1	
Ctenodiscus crispatus	–	–		–	–		1	0.1		1	0.03	
Echinoidea (sea urchins)	1	0.1		–	–		1	0.1		2	0.05	
Holothuroidea (sea cucumbers)	2	0.3		5	0.4		10	0.5		17	0.4	
Ophiuroidea (brittle stars)	–	–		3	0.3		3	0.2		6	0.1	
Ophiura sarsi	–	–	(0.4)	–	–	(0.9)	2	0.1	(1.1)	2	0.05	(0.73)
Vertebrata												
Osteichthyes												
Clupeidae (herrings)												
Clupea harengus pallasi	6	0.8		1	0.1		2	0.1		9	0.2	
Osmeridae (smelts)	3	0.4		2	0.2		4	0.2		9	0.2	
Mallotus villosus	–	–		–	–		1	0.1		1	0.03	
Gadidae (codfishes)												
Theragra chalcogramma	12	1.7		32	2.7		109	5.3		153	3.9	
Gadus macrocephalus	7	1.0		13	0.9		3	0.2		23	0.6	
Zoarcidae (eelpouts)	29	4.2		9	0.8		7	0.3		45	1.1	
Lycodes brevipes	–	–		–	–		3	0.2		3	0.08	
Scorpaenidae (rockfishes)	1	0.1		1	0.1		–	–		2	0.05	
Hexigrammidae (greenlings)												
Pleurogrammus monopterigius	–	–		–	–		2	0.1		2	0.05	
Cottidae (bullheads)	8	1.1		27	2.3		6	0.3		41	1.0	
Dasycottus setiger	–	–		–	–		2	0.1		2	0.05	
Hemilepidotus jordani	–	–		–	–		1	0.1		1	0.03	
Gymnocanthus sp.	–	–		–	–		6	0.3		6	0.1	
Agonidae (poachers)	–	–		3	0.3		17	0.8		20	0.5	
Bathymasteridae (ronquils)												
Bathymaster signatus	–	–		1	0.1		2	0.1		3	0.05	
Trichodontidae (sandfishes)												
Trichodon trichodon	–	–		4	0.3		2	0.1		6	0.1	
Cyclopteridae (lumpsuckers)	1	0.1		1	0.1		5	0.2		7	0.2	
Pleuronectidae (flatfishes)	22	3.2		21	1.8		40	1.9		83	2.1	
Atheresthes stomias	–	–		–	–		2	0.1		2	0.05	
Hippoglossoides elassodon	–	–		–	–		12	0.6		12	0.3	
Hippoglossus stenolepis	–	–		–	–		2	0.1		2	0.05	
Ammodytidae (sand lances)												
Ammodytes hexapterus	20	2.9		20	1.7		9	0.4		49	1.2	
Stichaeidae (pricklebacks)	14	2.0		–	–		10	0.5		24	0.6	
Crypacanthodidae (wrymouths)												
Lyconectes aleutensis	9	1.3		4	0.3		4	0.2		17	0.4	
Unidentified fishes	256	37.1	(55.9)	476	40.2	(51.9)	655	31.8	(44.1)	1387	35.3	(48.2)
Stomachs empty	8	1.6		59	5.0		184	8.9		251	6.4	

TABLE 2.—The importance of the snow crab, *Chionoecetes bairdi*, in the summer diet of Pacific cod. Analysis based on specimens from pots. Crab incidence is given for total number of cod examined; incidence as a percent of feeding cod given in parentheses.

Sampling date	Cod examined (no.)	Feeding cod (%)	Incidence of crabs		Crabs (no.)	Average crab occurrence in cod feeding on crabs
			Number	Percent		
26 June-3 August 1973	689	98.8	281	40.7 (41.3)	1,022	3.6
28 June-31 July 1974	1,183	95.0	427	36.2 (38.0)	1,033	2.4
30 June-27 July 1975	2,061	91.0	734	35.6 (39.1)	2,682	3.6
Total	3,933	93.6	1,442	36.7 (39.2)	4,737	3.3

TABLE 3.—Frequency and percent frequency of occurrence of food items in stomachs of *Gadus macrocephalus* collected July 1975 and 1976 by otter trawl near Kodiak Island, Alaska. N = number of stomachs examined. Subtotals in parentheses.

Food items	July 1975 N = 150		July 1976 N = 194		Total 1975-1976 N = 344	
	Freq.	% Freq.	Freq.	% Freq.	Freq.	% Freq.
Annelida						
Polychaeta	2	1.3	3	1.5	5	1.4
Mollusca						
Pelecypoda and Gastropoda	17	11.3	10	5.1	27	7.8
Cephalopoda	3	2.0	8	4.1	11	3.2
Arthropoda						
Crustacea						
Euphausiacea and Mysidacea	13	8.6	10	5.1	23	6.7
Isopoda	-	-	3	1.5	3	0.9
Amphipoda	14	9.3	15	7.7	29	8.4
Decapoda						
Pandalidae	16	10.7	24	12.4	40	11.6
Crangonidae	37	24.7	37	19.1	74	21.5
Unidentified shrimps	18	12.0 (47.4)	24	12.4 (43.9)	42	12.2 (45.3)
Majidae						
Chionoecetes bairdi	55	36.7	82	42.3	137	39.8
Unidentified crabs	13	8.7 (45.4)	23	11.9 (54.2)	36	10.5 (50.3)
Echinodermata	1	0.6	-	-	1	0.3
Vertebrata						
Osteichthyes						
Gadidae						
Theragra chalcogramma	6	4.0	7	3.6	13	3.8
Pleuronectidae	5	3.3	4	2.1	9	2.6
Ammodytidae						
Ammodytes hexapterus	20	13.3	13	6.7	33	9.6
Unidentified fishes	66	44.0 (64.6)	70	36.1 (48.5)	136	39.5 (55.5)
Stomachs empty	7	4.7	13	6.7	20	5.8

TABLE 4.—Comparison of percent frequency of occurrence of summer food groups in male and female *Gadus macrocephalus* caught by pots and trawls in the Kodiak Island area.

Food groups	Percent frequency of occurrence in: Pot-caught cod		Trawl-caught cod	
	Males	Females	Males	Females
Fishes	21.8	24.2	26.3	24.8
Crabs	22.0	19.3	24.2	20.9
Shrimps	15.1	14.2	15.4	24.7
Amphipods	10.0	14.3	4.1	4.3
Gastropods and pelecypods	5.0	4.7	3.3	4.5
Cephalopods	3.6	4.7	2.3	0.9
Euphausiids and mysids	2.1	4.0	4.0	2.7
Polychaetous annelids	1.4	3.1	0.3	1.1
Echinoderms	0.4	0.4	0.1	0.2
Isopods	0.2	0.2	0.5	0.4
Empty stomachs	4.4	2.0	2.8	3.0
Stomachs examined (no.)	2,106	1,827	188	156

other studies on Gadiformes (e.g., Homans and Vladykov 1954; Wigley 1956; Powles 1958; Wigley and Theroux 1965).

A significant difference (χ^2, $\alpha = 0.05$) was found for occurrence of food groups between years for each size group (Figure 2). The only similarity was among 33-52 cm fish between 1973 and 1975 and among 73-92 cm fish between 1974 and 1975. Some trends in frequency of food groups by cod size were apparent (Figure 2). Fishes and cephalopods increased in frequency with increasing cod size over all years while amphipods and polychaete worms decreased. Daan (1973) investigated the relative size of food items (crustaceans and fishes) used by the Atlantic cod, *G. morhua*, and found

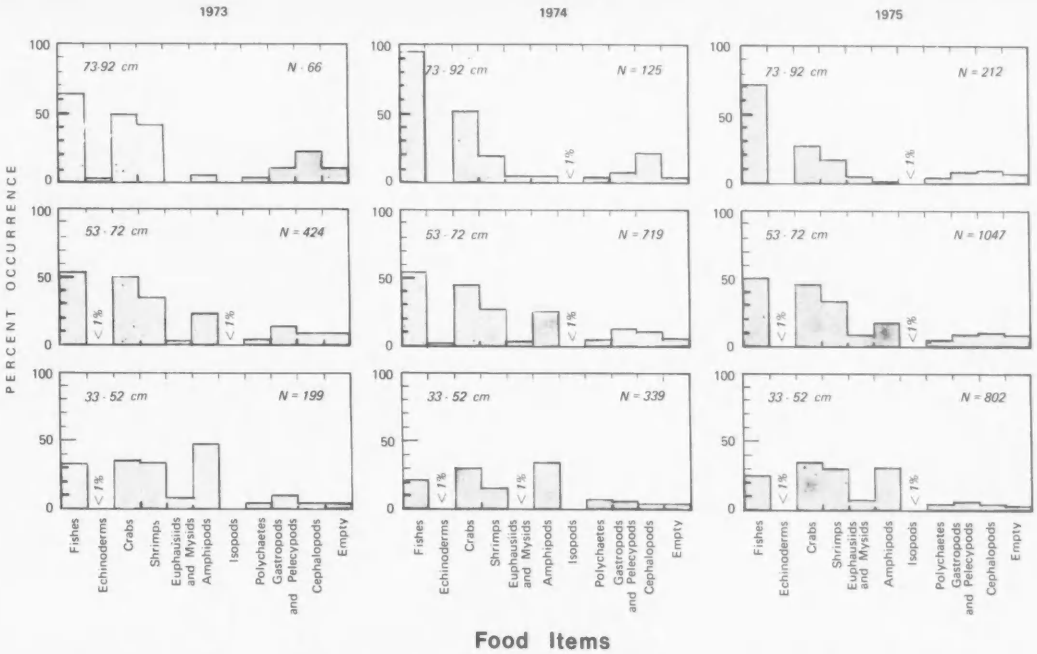

FIGURE 2.—Percent frequency of occurrence of summer food items within three size groups of pot-caught Pacific cod by year of collection—1973-75—near Kodiak Island, Alaska.

that smaller crustaceans were more commonly found in small cod while a gradual shift to a mixed diet of larger prey (primarily fishes) was noted for the larger fish. Arntz (1974) examined juvenile *G. morhua*, and found the most important food to be small crustaceans, mainly cumaceans (35.6% by weight of the total food consumed); fishes accounted for only 15.3% by weight of the total food consumed. This trend of large cod being more piscivorous than small cod has also been demonstrated by Powles (1958) and Rae (1967).

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A COMPUTER SOFTWARE SYSTEM FOR OPTIMIZING SURVEY CRUISE TRACKS[1]

Since 1972, the Southeast Fisheries Center, National Marine Fisheries Service, NOAA, has been conducting resource assessment surveys for groundfish in the northern Gulf of Mexico. Random sampling stations were selected and cruise tracks plotted by hand requiring several mandays of effort without assurance than an optimum cruise track had been chosen. Consequently, a computer routine was developed at the NMFS National Fisheries Engineering Laboratory, Bay Saint Louis, Miss., to satisfy two requirements: Generate a set of randomly selected sampling stations from a preestablished station grid and minimize the distance the vessel must travel to sample each station once. This paper presents the resultant routine, a comparison of results with actual cruises, and a discussion of other possible applications of the program.

Background

The problem of determining the optimum cruise track to sample a given set of stations can be restated as, "determining the shortest route from one point to another which allows a vessel to visit every station once." This problem is similar to one in the field of operations research generally referred to as "the traveling salesman problem." The original formulation of the problem was to minimize the time required by a traveling salesman to visit a number of cities and return home (Bellmore and Nemhauser 1968). Several algorithms have been developed which solve the problem exactly; however, computer storage and running time increase exponentially with the number of points to be visited. Because the groundfish surveys normally deal with station numbers in excess of 100, an heuristic method of solving the problem was selected. Lin and Kernighan (1973) at the Bell Telephone Laboratories (BTL) developed an approximate procedure for solving traveling salesman problems with large number of visitation points which appeared applicable to cruise track optimization.[2] The National Fisheries Engineering Laboratory obtained

[1]Contribution No. 78-19F from the Southeast Fisheries Center, National Marine Fisheries Service, NOAA, NSTL Station, MS 39529. MARMAP Contribution No. 154.

[2]To develop a feeling for the complexity of these problems, it should be noted that for a given number of stations, n, there are

a FORTRAN program from BTL and converted it to operate on a Univac[3] 1108 system at the National Aeronautics and Space Administration Computer Complex, Slidell, La.

Modifications to the BTL algorithm were made to satisfy requirements of the groundfish survey program. Most internal modifications were fairly general so that the program could be used for other areas and purposes. Specifics of grid locations and random selection requirements were stored on magnetic tape in a separate master file. The program, as presently configured, can handle up to 150 stations; however, 300 stations could be handled using extended core storage.

Algorithm Description

Assume a number of stations (n) have been selected, either randomly or specifically. There are a total of $n(n-1)/2$ links between the n stations. The object is to find an n-subset of these links such that (a) each station is sampled exactly one time, and (b) the total distance traveled is a minimum. A sequence of links satisfying (a) is called a tour; if it also satisfies (b), it is the optimum tour.

The optimization algorithm begins by computing all $n(n-1)/2$ distances and storing them in a matrix. A completely random tour is generated to use as a starting point. An attempt is then made to find two sets of links $X = x_1, x_2 \ldots x_k$ *and* $Y = y_1, y_2 \ldots y_k$ such that if the links in X are replaced with the links in Y, the result gives a tour of a shorter distance. This is done by identifying x_1 and y_1 as the "most-out-of-place" pair, setting them aside, then proceeding with x_2 and y_2, x_3 and y_3, and so on.

A criterion is then used to determine how many pairs of links are to be exchanged. This criterion can be explained as follows: Let the length of x_i and y_i be dx_i and dy_i, and $g_i = dx_i - dy_i$. This determines the gain (shorter distance) by exchanging x_i with y_i. After examining a sequence of proposed exchanges $x_1, x_2 \ldots x_k$ and $y_1, y_2 \ldots y_k$ with their corresponding gains $g_1, g_2 \ldots g_k$, the actual value of k that defines the number of sets to exchange is the one for which $g_1 + g_2 + \ldots + g_k$ is always zero or negative. This indicates the solution is a local optimum based on the fact that if a sequence of numbers has a positive sum, there is a cyclic permutation of these numbers such that every partial sum is positive. Hence, the algorithm looks for sequences of g_i's whose partial sum is always positive, reducing the number of sequences that need to be examined. This means that the value of k, which gives the number of links to be exchanged, is determined when $G^* = \sum_{j=1}^{k} g_j \leq 0$, i.e., when the partial sum of the gains fails to remain positive. These links are then exchanged and the process of selecting new links to be exchanged begins again at $i = 1$. When all possibilities have been tried, the tour length is recorded. The program generates a new random initial tour and the entire process begins again. Eleven distinct solutions are produced in this manner, and the tour with the shortest length is considered the optimum solution. Program operation can best be understood by a simple example.

Assume that n stations are selected and a random tour generated (Figure 1a5. The black dots represent the stations and the circle represents the random tour. Any station S_1 is selected and S_2 is designated as an adjacent station in the tour. The link connecting the two stations is designated

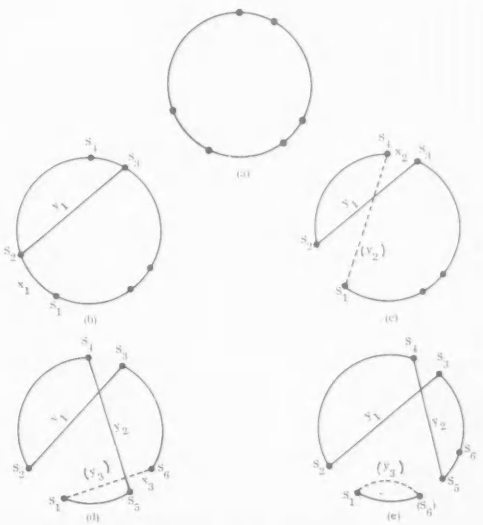

FIGURE 1.—Example of the algorithm operation (modified from Lin and Kernighan 1973).

$(n-1)$ factorial possible cruise tracks that satisfy the criterion of sampling all stations once and returning to starting position (e.g., if $n = 101$, the number of possible solutions is 9.3326×10^{157}).

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

as x_1 as shown schematically in Figure 1b. The station closest to S_2 is designated as S_3 and y_1 is the link joining S_2 and S_3. The link y_1 is not permitted to be either of the links already connected to S_2. The gain criterion is then calculated as $g_1 = dx_1 - dy_1$. If this is negative, S_2 is designated as the other neighbor of S_1 in the tour. If g_1 is positive, S_4 is designated as one of the tour neighbors of S_3 as shown in Figure 1c. If y_2 were chosen to join S_4 with S_1, the result would be a tour. The gain criterion is then calculated as $g_2 = dx_2 - dy_2$. If $g_1 + g_2 > 0$, the original tour could be improved by exchanging x_1 and x_2 with y_1 and y_2, respectively. This potential improvement, which results from closing up the tour immediately ($G^* = g_1 + g_2$), is then stored. Now S_5 is chosen as the nearest neighbor of S_4, and y_2 is designated as the link connecting the two stations. Station S_5 is not permitted to be either of the stations already connected to S_4. Figure 1d shows there is only one choice for station S_6 and the link x_3 such that if S_6 is connected to S_1, a tour remains. If S_6 were chosen as the other neighbor of S_5 in the original tour, closing up S_6 to S_1 would result in a tour of two disconnected pieces (Figure 1e). The gain associated with closing up immediately (connecting S_6 with S_1) is then compared with that obtained by joining S_4 to S_1 (G^*). The link connecting S_6 to S_1 is designated as y_3. The gain criterion is then calculated as $g_3 = dx_3 - dy_3$. If $g_1 + g_2 + g_3 \leq G^*$ (G^* is the best improvement thus far), there is no improvement, so the number of links (k) to be profitably exchanged is defined as $k = 2$. If $g_1 + g_2 + g_3 > G^*$, however, a new station S_7 and link x_4 are selected and the process is continued.

A limited backtracking feature of the program is included for the case when $G^* = 0$ (i.e., no improvement can be made). The link y_2 was chosen (Figure 1d) to join S_5 to S_4 as the closest station to S_4. When no improvement is made at some stage ($G^* = 0$), new links y_2 are considered in order of increasing length to a maximum of five choices. If still no improvement is found, the five y_1 links are examined in order of increasing length. When G^* cannot be improved, and the value k determined, a new initial station S_1 is selected and the process repeated. The procedure ends when all n stations have been examined. A new random tour is generated, and each station is examined as an S_1 again in the same manner. This limited backtracking significantly increases program effectiveness.

The computational procedure has other features that improve the calculations and reduce running time; such as limited foresight to the next links to be broken, allowance for nonsequential link exchanges, and elimination from computation of those links previously recorded in good tours. For a more complete description of the algorithm, see Lin and Kernighan (1973).

Results

Station Description

Separate station grids lere used for areas east and west of the Mississippi River Delta. A station consisted of a rectangle, lat. 2′30″ by long. 2′30″, within which three trawl tows were made. Stations were identified and located at the center point of the rectangle.

The station grid for the West Delta area consisted of an area extending from long. 89°30′W to 91°30′W (Figure 2). The station grid for the East Delta area consisted of a primary and secondary zone extending between long. 88°00′W and 89°30′W and long. 79°30′W and 88°00′W (Figure 3). Each area was limited by the 9.2-m (5-fm) and 92-m (50-fm) depth contours. Stations were excluded from random selection in both areas because of navigation and trawling hazards, and areas of known low groundfish densities.

Random Selection

Station number, latitude, and longitude were stored in a master grid file for each area. Input to station selection for the West Delta region was the number of stations to be sampled. This region had 780 stations. For the East Delta area, the number of stations must be specified separately for the primary and the secondary zones—there were 555 stations in the primary zone and 139 in the secondary region. Station selection was performed by a random number generator which selected stations based on the number required for each area.

Cruise Track Optimization

Requirements for an optimized cruise track were different for the areas east and west of the delta. A round-trip track was desired for the West Delta area, while a one-way calculation was desired for the East Delta area. The latter consisted of the shortest route from a designated starting point near Pascagoula. Miss., through each selected station and ending at a point near the mouth of the Mississippi River.

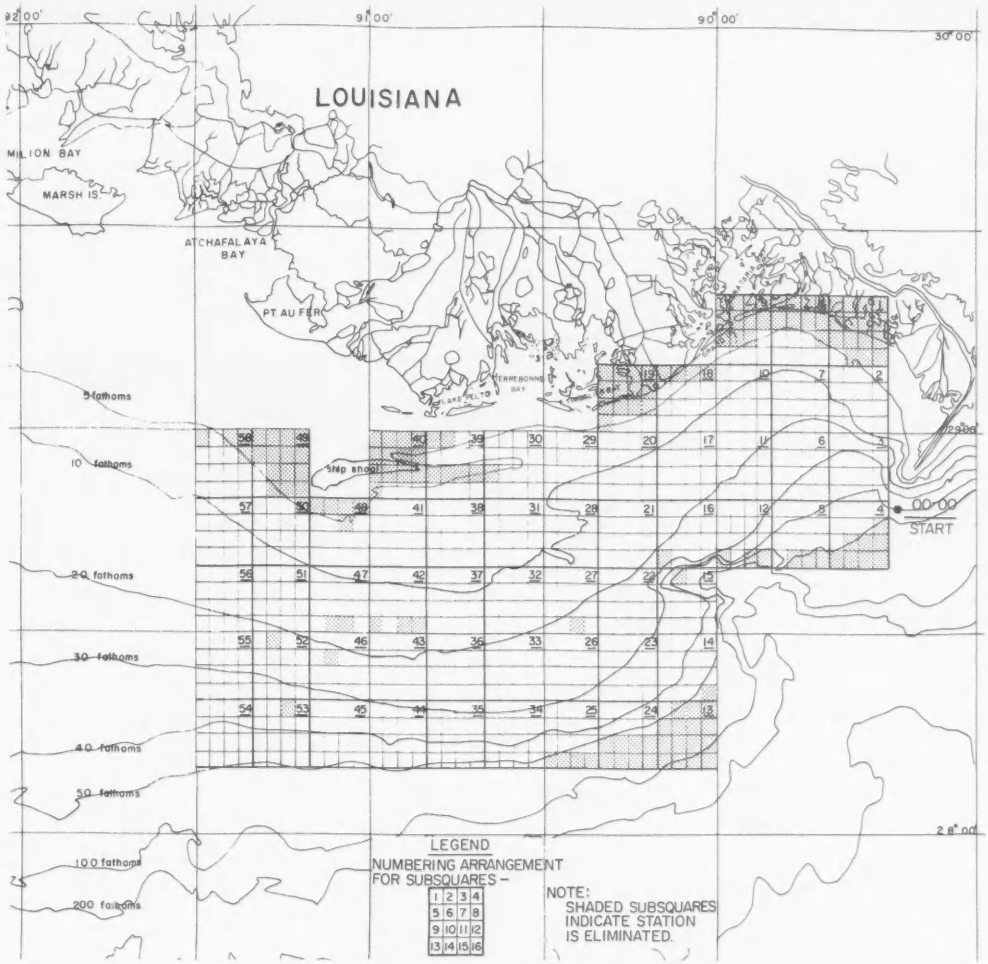

FIGURE 2.—Master station grid for groundfish survey sampling in northern Gulf of Mexico - West Delta area. Dot labeled 00-00 is start and end point for round-trip cruise track optimization.

Since the grid used in the calculations was square, a coefficient was included to account for differences in absolute distance for one unit of longitude vs. one unit of latitude. The coefficient used for optimizing groundfish survey tracks is 52.10/59.85, which is the ratio of the distance in nautical miles for 1° of longitude to that for 1° of latitude at lat. 30°N. All longitudinal Cartesian coordinate distances were multiplied by this coefficient before calculations began.

For the West Delta area, the cruise track was optimized from a point located just east of the primary survey area (Pascagoula station number 00-00) through all randomly selected stations, returning to the starting point. The optimization program computed 11 solutions and the best route in terms of the shortest distance was selected. Output consisted of a listing of stations in proper sampling order, and a plot of the stations and optimum cruise track with every fifth station labeled.

The starting point of the cruise track was south of Pascagoula for the East Delta area. Optimization was done for a cruise track that visited all

randomly selected primary and secondary stations and terminated at a point near the Mississippi River Delta designated 99-99 (Figure 3). Outputs were the same as for the West Delta except for treatment of the stations randomly selected which appear in blocks 45, 46, 47, and 48. These were not included in the optimized cruise track, but were listed at the end of the optimized cruise track listing. The stations in these blocks were added to the end of the optimized cruise track and plotted as individual points labeled with their Pascagoula number.

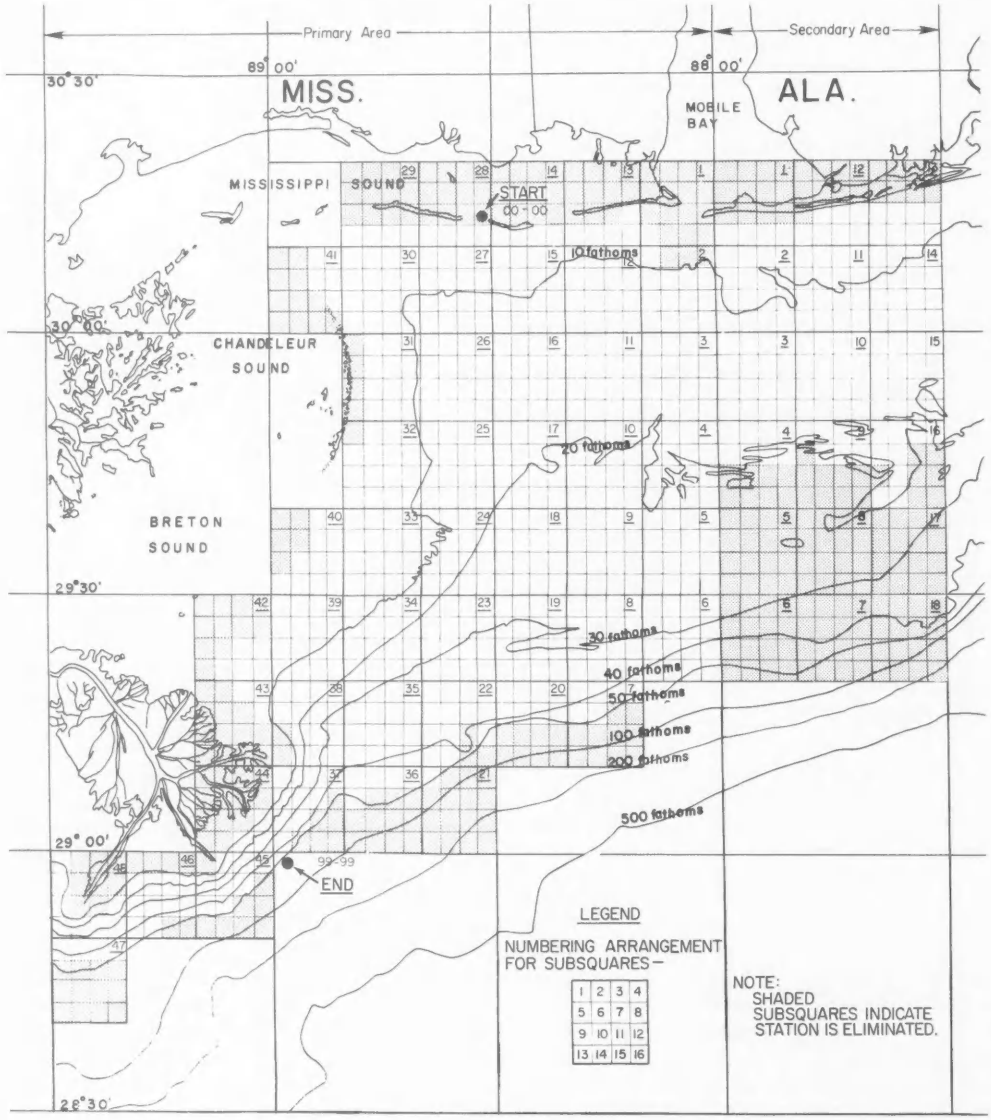

FIGURE 3.—Master station grid for groundfish survey sampling in northern Gulf of Mexico - East Delta area. Dot labeled 00-00 is starting point and dot labeled 99-99 is end point for one-way cruise track optimization. Primary and secondary areas are indicated by arrows at top of figure.

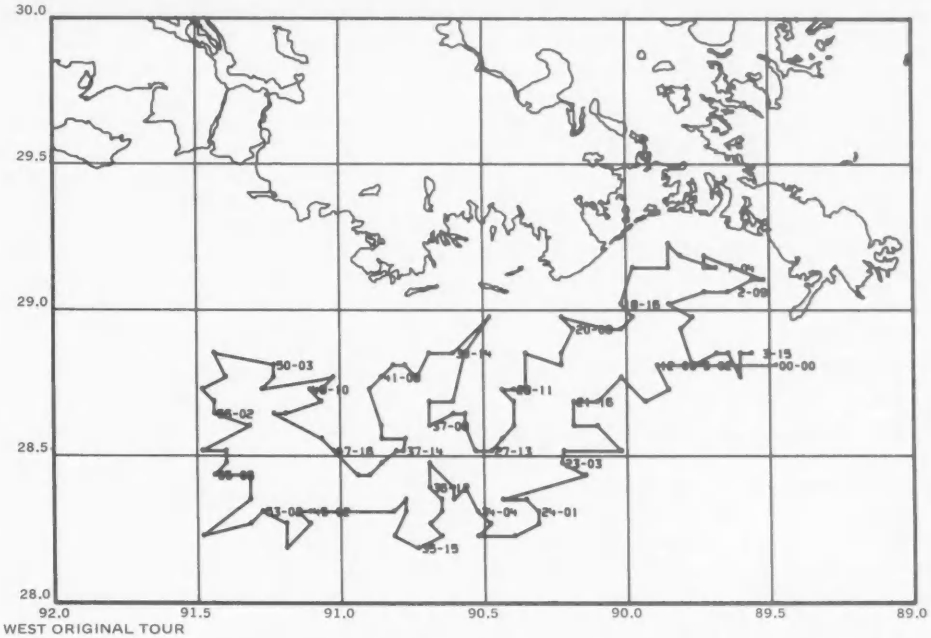

FIGURE 4.—Actual cruise track followed for West Delta area, FRV *Oregon II* cruise 55. Every fifth station is labeled.

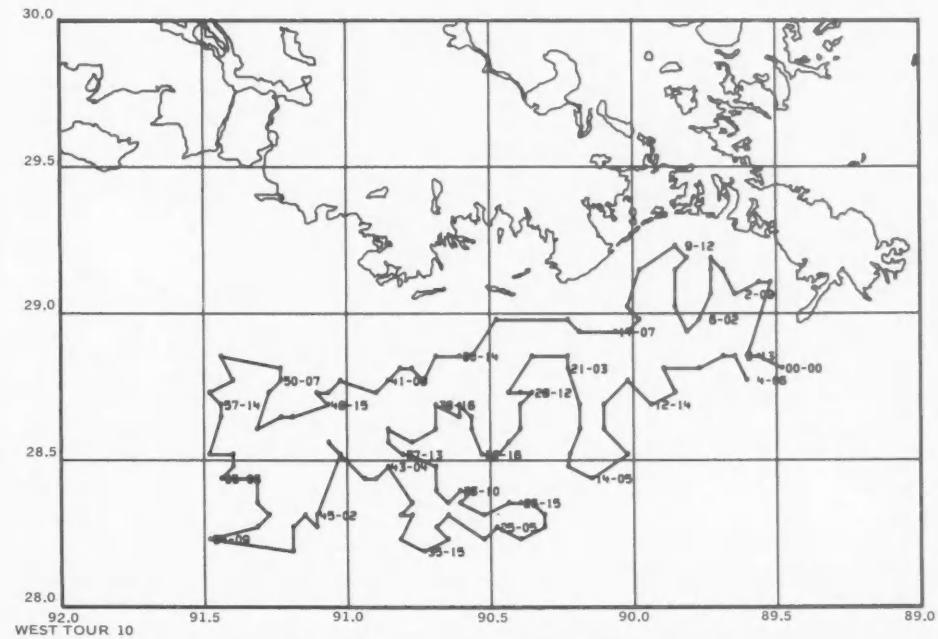

FIGURE 5.—Optimized cruise track for West Delta area, FRV *Oregon II* cruise 55. Every fifth station is labeled.

Test Case and Sample Products

The optimization program was tested to compare computational results with a cruise track actually followed during a survey—FRV *Oregon II* cruise 55, 5-29 November 1974.

West Delta

The 126 stations sampled during cruise 55 for the West Delta area were entered in the order they were sampled (Figure 4), and the total distance (in grid units) was calculated to be 254. Each grid unit was equivalent to approximately 4.6 km; thus, the total distance was about 1,176 km.

Eleven computations were performed on these stations by the optimization program, and a minimum length of 233 grid units (approximately 1,078 km) occurred three times. It can be said with confidence the optimum tour (Figure 5) represented an 8.3% improvement over the actual cruise track. Distances were calculated from the center of each subsquare; therefore, the actual dis-

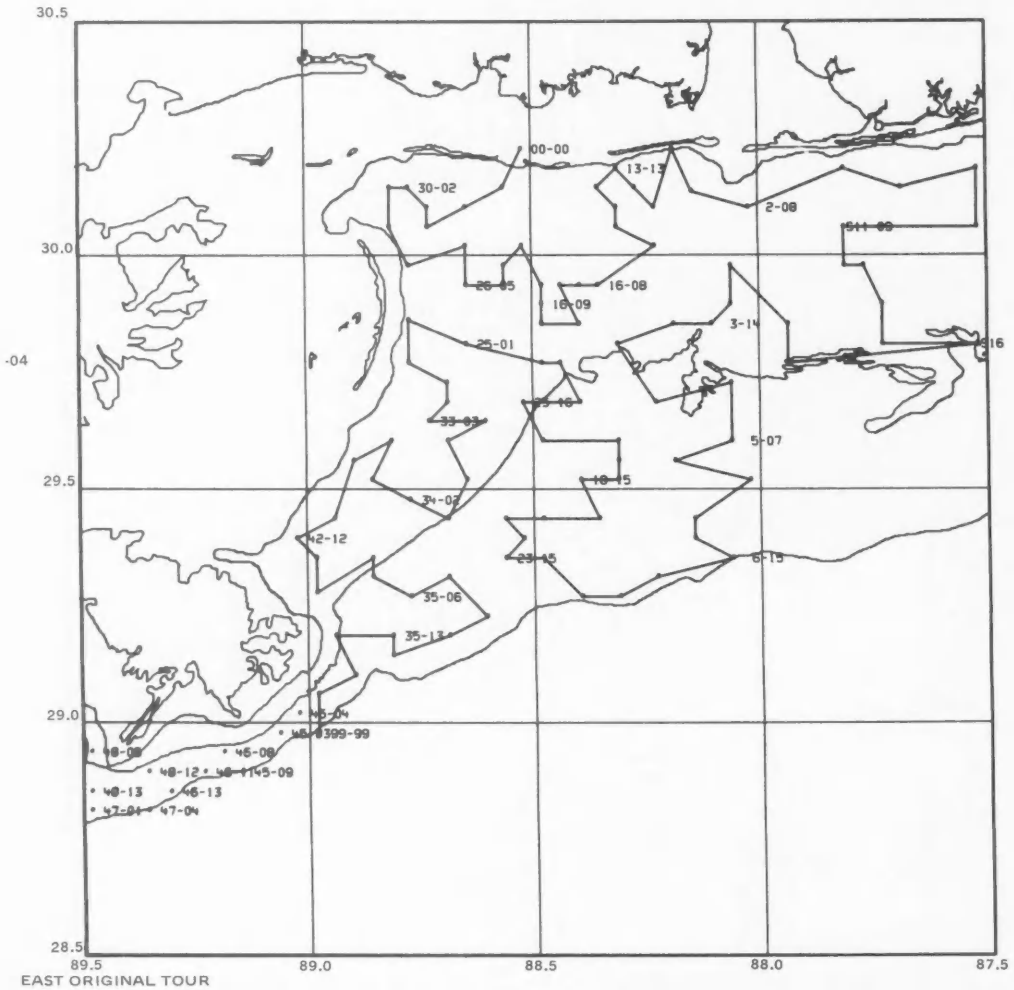

FIGURE 6.—Actual cruise track followed for East Delta area, FRV *Oregon II* cruise 55. Every fifth station is labeled. Station numbers listed at lower left are those not included in optimization calculations.

tance would be decreased by the vessel cutting corners of the subsquares. Calculations for the 126 stations on the Univac 1108 system used about 60K of core storage and required 2 min of Central Processing Unit (CPU) time.

East Delta

Cruise 55 was used to test the program for the East Delta area also. Of 116 stations sampled, 105 were included in the computation of an optimum one-way cruise track. The other 11 stations were located in blocks 45, 46, 47, and 48. They were, however, added to the end of the optimized listout, plotted, and labeled on the cruise track plot. The actual cruise track distance for the 105 stations was 229 grid units (approximately 1,061 km) (Figure 6). The optimized one-way path was calculated to be 216 grid units (1,000 km), an improvement of 5.8% (Figure 7). Calculations for the 105 stations used 60K of core storage and required 66 s of CPU time.

FIGURE 7.—Optimized cruise track for East Delta area, FRV *Oregon II* cruise 55. Every fifth station is labeled. Station numbers listed at lower left are those not included in optimization calculations.

Discussion

The basic optimization program has the capability and inherent versatility to be utilized for a wide range of applications. The round-trip capability can be modified to a one-way path calculation as was done for the East Delta portion of the groundfish survey by manipulating the distance matrix. Cartesian integrity of the start-stop points is kept intact but the distance between the two stations is set equal to zero in the distance matrix. The program then calculates the optimum tour as if the start-stop points were very close together when, in fact, they are not.

There is no requirement that distance be the optimization parameter. Factors such as cost, time, or suitable weighted combinations of other variables could be used to compute a cruise track considered optimum for specific user requirements. Also, there is no requirement that the problem be symmetric or Cartesian in nature. For example, the distance (cost, time, etc.) in going from station A to station B need not be equal to that from station B to station A. Applications of these characteristics and other distance matrix manipulations include:

1) The "cost" in going from station to station in the presence of strong currents, such as the Gulf Stream, could be adjusted. "Downstream" directions from station to station would be given preferential status for computing the optimum cruise track.
2) In some situations, it may be desirable to group selected stations to be sampled preferentially as a subset or subsets of the total station pattern. This might occur if certain sampling areas had a higher priority than others because of biological and/or environmental considerations.
3) Actual curvilinear distances between stations could be entered into the distance matrix when sampling in areas near the coast. This would be done for station pairs connected by a straight line that passes across land.
4) If the number of stations exceeds the present 150 maximum allowable (300 with extended core storage), and it is possible to divide them into subgroups, the problem is limited only by CPU restrictions.

Many variations of the optimum cruise track theme could be solved with this program and the requirements are usually unique to a particular problem or investigation.[4] The examples demonstrate the types of problems that could be solved. Simple problems, such as those solved for the groundfish survey, can be improved about 7% over manually produced cruise tracks.

Improvements obtained using the optimized cruise track for the cited application are not dramatic, but would be significant over a long time period and/or extensive cruising distance. The program eliminates selecting stations from random number tables and hand plotting the cruise track, which may require several man-days

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[4]Inquiries regarding possible uses and applications of this system should be directed to the Director, Southeast Fisheries Center National Fisheries Engineering Laboratory, National Space Technology Laboratories, NSTL Station, MS 39529.

Notices

NOAA Technical Reports NMFS published during the first 6 mo of 1978.

Circulars

409. Marine flora and fauna of the northeastern United States. Copepoda: cyclopoids parasitic on fishes. By Ju-Shey Ho. February 1978, iii + 12 p., 17 fig.

410. The 1976 *Ceratium tripos* bloom in the New York Bight: causes and consequences. By Thomas C. Malone. May 1978, iv + 14 p. 17 fig., 1 table.

411. Systematics and biology of the tilefishes (Perciformes: Branchiostegidae and Malacanthidae), with descriptions of two new species. By James K. Dooley. April 1978, v + 78 p., 44 fig., 26 tables.

412. Synopsis of biological data on the red porgy, *Pagrus pagrus* (Linnaeus). By Charles S. Manooch III and William W. Hassler. May 1978, iii + 19 p., 12 fig., 7 tables. Also FAO Fisheries Synopsis No. 116. For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402 Stock No. 003-017-00418-0.

413. Marine flora and fauna of the northeastern United States. Crustacea: Branchiura. By Roger F. Cressey. May 1978, iii + 10 p., 15 fig. For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402 Stock No. 003-017-00419-8.

Special Scientific Report—Fisheries

719. Seasonal description of winds and surface and bottom salinities and temperatures in the northern Gulf of Mexico, October 1972 to January 1976. By Perry A. Thompson, Jr. and Thomas D. Leming. February 1978, iv + 44 p., 43 fig., 2 tables. For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402 Stock No. 003-017-00414-7.

720. Sea surface temperature distributions obtained off San Diego, California, using an airborne infrared radiometer. By James L. Squire, Jr. March 1978, iii + 30 p., 15 fig., 1 table, 90 app. fig. For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402 Stock No. 003-017-00415-5.

721. National Marine Fisheries Service survey of trace elements in the fishery resource. By R. A. Hall, E. G. Zook, and G. M. Meaburn. March 1978, iii + 313 p., 5 tables, 3 app. fig., 1 app. table.

722. Gulf menhaden, *Brevoortia patronus*, purse seine fishery: catch, fishing activity, and age and size composition, 1964-73. By William R. Nicholson. March 1978, iii + 8 p., 1 fig., 12 tables.

723. Ichthyoplankton composition and plankton volumes from inland coastal waters of southeastern Alaska, April-November 1972. By Chester R. Mattson and Bruce L. Wing. April 1978, iii + 11 p., 1 fig., 4 tables, 1 app. table.

724. Estimated average daily instantaneous numbers of recreational and commercial fishermen and boaters in the St. Andrew Bay system, Florida, and adjacent coastal waters, 1973. By Doyle F. Sutherland. May 1978, iv + 23 p., 31 fig., 11 tables.

725. Seasonal bottom-water temperature trends in the Gulf of Maine and on Georges Bank, 1963-75. By Clarence W. Davis. May 1978, iv + 17 p., 22 fig., 5 tables.

NOAA Technical Reports NMFS are available free in limited numbers to Federal and State government agencies. They are also available in exchange for other scientific and technical publications in the marine sciences. Individual copies, if available, may be obtained by purchase from the Superintendent of Documents or by writing to User Services Branch (D822), Environmental Science Information Center, NOAA, Rockville, MD 20852.

Data on fisheries subjects accessioned through NMFS by NODC during the first 6 mo of 1978.

Drift bottle, northwestern Gulf of Mexico, February 1962 to December 1963. Fifty data sheets in manuscript form. By R. F. Temple and John R. Martin, Gulf Fisheries Center, NMFS. Ref: NAPIS 78-0035.

This material is available from the National Oceanographic Data Center (D7514), National Oceanic and Atmospheric Administration, Washington, DC 20235.

ERRATA

Fishery Bulletin, Vol. 76, No. 2

Fletcher, R. Ian., "Time-dependent solutions and efficient parameters for stock-production models," p. 377-388.

1) Page 377, right column, line 4, correct line to read:
growth rate k and B_∞, Graham's formula for latent

2) Page 378, left column, Equation (2), correct equation to read:

$$\dot{P}(B) = c_1 B + c_2 B^n, \qquad (2)$$

3) Page 378, left column, line 14, correct line to read:
antecedents of this analysis appear there.

4) Page 378, right column, line 7, correct line to read:
by average effort $\bar{f}$ on the assumption that $F =$

5) Page 379, left column, the equation that immediately follows Equation (1a), correct equation to read:

$$k = \frac{4m}{B_\infty} \left[\equiv 4 \frac{\dot{P}_{\max}}{B_{\max}} \right].$$

6) Page 381, right column, line 4, correct line to read:
Equation (6), $\dot{B} = 0, F = F_1$ and $B = B_1$. If we now

7) Page 381, right column, line 28, correct line to read:
$F = 2m/B_\infty$; stock size $B(t) \rightarrow p$ (p being

8) Page 383, right column, Equation (15), correct equation to read:

$$\dot{B} = \gamma m \left[\frac{B}{B_\infty} \right] - \gamma m \left[\frac{B}{B_\infty} \right]^n - FB. \qquad (15)$$

9) Page 383, Figure 5, caption under right figure, line 3, correct line to read:
$\dot{P}_{\max}$ in Equation (12)].

10) Page 385, left column, line 14, correct line to read:
then $B(t) \rightarrow p$ and $\dot{Y} \rightarrow m$, irrespective of initial con-

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Manuscripts submitted to the *Fishery Bulletin* will reach print faster if they conform to the following instructions. These are not absolute requirements, of course, but desiderata.

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In the **text,** *Fishery Bulletin* style, for the most part, follows that of the *U.S. Government Printing Office Style Manual.* Fish names follow the style of the American Fisheries Society Special Publication No. 6, *A List of Common and Scientific Names of Fishes from the United States and Canada,* Third Edition, 1970.

Text footnotes should be typed separately from the text.

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Do not send original drawings to the Scientific Editor; if they, rather than the photographic reductions, are needed by the printer, the Scientific Publications Office will request them.

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Acknowledgments, if included, are placed at the end of the text.

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